# Modelling of sexual reproduction in a world of diverse and limited resources

Modellierung der sexuellen Reproduktion in einer Welt mit diversen limitierten Ressourcen
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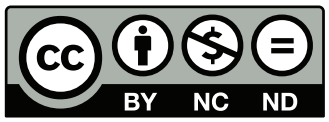

*For Timo*

## Zusammenfassung

Sexuelle Reproduktion ist durch doppelte Kosten benachteiligt gegenüber asexueller Reproduktion. Trotzdem vermehren sich die meisten Spezies sexuell. Dieses Paradoxon ist seit C. Darwin (1859) ein Rätsel in der Evolutionsbiologie. In dieser Arbeit wird ein Modell vorgestellt, das sowohl die weite Verbreitung sexueller Reproduktion als auch die geographische Parthenogenese erklärt. Geographische Parthenogenese ist die Beobachtung, dass viele normalerweise sexuelle Spezies sich am Rand ihres Verbreitungsgebiets asexuell vermehren, beispielsweise im Norden, in großer Höhe oder am Übergang zur Wüste. Da die Verfügbarkeit von Ressourcen maßgeblich das Populationswachstum bestimmt, werden Ressourcen explizit in dem Modell berücksichtigt. Der Vorteil der sexuellen Individuen besteht darin, dass sie genetisch verschiedene Nachkommen produzieren, die andere Ressourcen konsumieren können als ihre Eltern.

Das Modell beinhaltet ein breites Spektrum von langsam nachwachsenden Ressourcen. In diesem Modell gewinnt über weite Parameterbereiche die sexuelle Reproduktion. Die asexuelle Reproduktion gewinnt nur bei hoher Mortalität, geringer Ressourcenvielfalt oder schnellem Ressourcenwachstum. Wird dem Modell ein räumlicher Gradient in der Mortalität und Ressourcenvielfalt auferlegt, so wie er beispielsweise von Süden nach Norden vorliegt, dominiert die sexuelle Reproduktion im Bereich mit niedriger Mortalität und vielfältigen Ressourcen und die asexuelle Reproduktion im Bereich mit hoher Mortalität und geringer Ressourcenvielfalt.

Die Ergebnisse des Modells sind unabhängig von den genetischen Implementationen. Das Modell erklärt die weite Verbreitung von sexueller Reproduktion nicht nur für kurzlebige Spezies sondern auch für langlebige Organismen, die sich im Leben mehr als einmal reproduzieren. Die Evolution sexueller Reproduktion ist bislang nicht für langlebige Organismen untersucht worden, weil diese Untersuchung ein anderes Forschungsthema involviert, nämlich die Life-History-Theorie.

Wir konstruieren hierfür ein mathematisches Modell eines Consumer-Resource-Systems (Yodzis and Innes, 1992), das auf der metabolischen Theorie der Ökologie basiert. Anhand dieses Modells werden die wichtigsten Merkmale des Lebenszyklus, wie z.B. das Alter bei der ersten Fortpflanzung, die Anzahl der Nachkommen und die Lebenserwartung des Organismus, abgeleitet. Die Individuen reifen später und leben länger in Populationen mit größerer Körpermasse, kleinerer Konsumrate oder langsam nachwachsenden Ressourcen. Außerdem wird in diesem Modell Cope's Gesetz demonstriert, d. h., im Laufe der Evolution nimmt die Körpermasse von adulten Individuen tendenziell zu.

Wird das Modell in das Structured-Resource-Modell (Scheu and Drossel, 2007) integriert, dann kann dabei sogar die Abwesenheit der asexuellen Reproduktion unter Säugetieren und Vögeln aus ökologischer Sicht erklärt werden. Der Vorteil der sexuellen Reproduktion ist für langlebige Lebewesen größer im Vergleich zu kurzlebigen Spezies. Im Falle von kurzlebigen Spezies liefert das Modell eine starke Beschränkung der gleichzeitig am selben Ort überlebenden Nachkommen, die gleichzeitige Nutzung aller Ressourcen vermeidet. Im Falle von langlebigen Organismen überwiegt die sexuelle Reproduktion auch wenn viele Ressourcen gleichzeitig ausgebeutet werden.

## Abstract

Evolution is based on reproduction and survival of offspring. Reproduction in most organisms is sexual, i.e., a gamete sexually produced by a female thereby fuses with a gamete produced by a male to form progeny of the next generation. The evolution of sex has drawn attention since C. Darwin (1859), but remains enigmatic until today. Sexual reproduction suffers an inevitable disadvantage of a factor of two in comparison with asexual reproduction (Williams, 1975). In a sexual population, only one of the two sexes is capable of bearing young. Over the century, several hypotheses and models have been proposed to explain the maintenance of sexual reproduction. However, none of them has been commonly approved. Recently, Scheu and Drossel (2007) introduced a structured resource model that is based on limited and structured resources combined with stochastic effects. The advantage of sexual individuals in this model is the ability to produce offspring which can exploit new and underutilized resources. In this model asexuality wins over sexuality only when mortality is high, resource diversity is low, resources regrow fast, or many different genotypes are allowed to coexist at the same place. By adding a spatial structure into this model, we obtain a pattern resembling geographic parthenogenesis, i.e., sexuals prevail in central regions of low mortality or high resource diversity, while asexuals prevail at the boundary of species' range, where mortality is high or resource diversity is low.

In order to apply the structured resource model to long-lived organisms, we construct a mathematical model for a long-lived consumer species and its resources. The model takes into account the allometric scaling of consumption, metabolism, and mortality with consumer body mass. Mortality is assumed to be density dependent, and the dynamics of resources are explicitly modelled. We explore thereby the consequences of metabolic theory on life histories and life history evolution. We find that populations that have more or faster growing resources have a shorter life span and a higher mortality. Moreover, populations with a larger adult body mass have a larger number of offspring per female and a larger biomass density in this model. When we allow the adult body mass to evolve, it increases with time without limits. When we allow the offspring body mass to evolve, it becomes smaller. Both trends result from the allometric scaling of mortality and are kept in limits by other trade-offs than those included in our model.

By combining the two ecological models we find sexual long-lived organisms prevailing over asexual long-lived organisms in regions of low mortality, high resource diversity, or low resource growth rate. The advantage of sexual reproduction is larger in long-lived organisms compared to the advantage of sexual reproduction in annual organisms. In populations of long-lived organisms the offspring generation directly competes with the parent generation for resources, while there is only direct competition among siblings in populations of annual species. Therefore, asexual clones and parthenogenetically produced offspring suffer from more severe intraspecific competition in long-lived organisms. This is consistent with the dominance of sexual reproduction in large long-lived organisms and may provide an ecological explanation for the absence of asexual reproduction in birds and mammals. It might well be that in the evolutionary past of animals, such as vertebrates, the need to parthenogenetically produce offspring has almost completely vanished.

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# 1 Introduction

The maintenance of sexual reproduction has been one of the most controversial topics in evolutionary biology, and the debate continues until today. The debate started in the 18th century after Bonnet's discovery that females are able to produce offspring without being fertilized by males (Fournier *et al.*, 2005; Watts, 2006), i.e., by parthenogenesis[i]. This discovery refuted the spermism model of preformation theory that claimed that offspring develop from a tiny fully-formed embryo contained within the head of a sperm cell, and gave support to the ovist model that claimed that the pre-formed embryo is contained in the egg. After parthenogenetic reproduction had gained acceptance, Thomas Henry Huxley stated the problem with unprecedented clarity: "Time was when the difficulty of the physiologist lay in understanding reproduction without the sexual process. At the present day, it seems to me that the problem is reversed, and that the question before us is, why is sexual union necessary?" (T. Huxley, 1858) Charles Darwin realized the magnitude of the problem, but he left its solution to future generations as the genetic basis of sexual reproduction was yet unknown. "We do not even in the least know the final cause of sexuality: why new beings should be produced by the union of the two sexual elements, instead of by a process of parthenogenesis ... The whole subject is as yet hidden in darkness." (C. Darwin, 1962) Since then, many hypotheses have been proposed to explain the maintenance and prevalence of sexual reproduction. Weismann (1889) was the first to realize that the function of sexual reproduction is basically the mixis[ii] of genotypes. He assumed that the advantage of producing diverse offspring is related to evolutionary novelty: "I do not know what meaning can be attributed to sexual reproduction rather than the creation of hereditary individual characters to form the material upon which natural selection may work." The idea that the advantage of sex lies in the creation of genetic diversity was also expressed by Guenther (1906), Fisher (1930), and Muller (1932). It had in fact been foretold by Erasmus Darwin in the 18th century: "From the sexual, or amatorial, generation of plants new varieties, or improvements, are frequently obtained; as many of the young plants from seeds are dissimilar to the parent, and some of them superior to the parent in the qualities we wish to possess... Sexual reproduction is the chef d'oeuvre, the master-piece of nature." (E. Darwin, 1800)

## 1.1 The paradox of sexuality

The maintenance of sexuality had been considered as clarified by group selection arguments, i.e., the remarkableness of sex lies in its beneficial effect on the population or the species, rather than on the individuals (Weismann, 1889, p.281). Yet after the fundamental critique of Williams on models based on group selection arguments (Williams, 1966), novel explanations were needed. This need was reinforced by realizing the extraordinarily high cost associated with sexual reproduction (Table 1.1). This cost has a number of names: cost of sex, cost of meiosis, cost of males, and it is well known as the 'twofold cost of sex'. This cost is due to

[i] **Parthenogenesis** in Glossary.

[ii] **Mixis** in Glossary.

**Table 1.1.:** Inventory of the costs of sex (from Lewis (1987))

| |
|---|
| I. Costs not derived from anisogamy |
| 1) Recombination |
| 2) Cellular-Mechanical costs |
| a. Meiosis[iii] |
| b. Syngamy |
| c. Karyogamy |
| 3) Fertilization |
| a. Exposure to risk |
| b. Minimal density for reproduction |
| II. Costs derived from anisogamy |
| 1) Genome dilution (cost of males) |
| 2) Sexual selection |
| a. Sexual competition (conflict, exposure) |
| b. Dual phenotypic specialization |

the contribution of male genetic material to a zygote (Lewis, 1987). Compared with asexual females, sexual females contribute only half of the genetic material to each offspring, and thus encounter a large loss in propagation efficiency. Moreover, the material existence of males requires a twofold investment of the sexual female organisms in case of an equal sex ratio, since the sexual females have to allocate half of their reproductive investment to produce males that do not deliver offspring. Given an asexual and a sexual population of the same female fecundity, the asexual females propagate themselves twice as fast as the sexual females (Fig. 1.1). Associated with the high cost, shouldn't sex be selected against and eliminated whenever it arises in a community of asexual organisms? Yet this is not the case. The paradox of sex leaves us with the task to explain the maintenance and prevalence of sexual reproduction despite the twofold cost of sex, i.e., to identify and evaluate the vital advantage of sexual reproduction.

## 1.2 Theories of sex

### 1.2.1 Muller's ratchet

A considerable body of literature deals with the genetic advantages of sexual reproduction due to avoiding the accumulation of deleterious mutations (Keightley and Otto, 2006; Muller, 1964), or the advantages of segregation in populations with a high inbreeding rate (Otto, 2003). Muller (1964) originated the idea and referred to it as a 'ratchet' mechanism. Disregarding advantageous mutations, he found that an asexual population can never get to contain a load of mutations smaller than that already accumulated in its lineages. Sexual population, on the other hand, can be swept clean of newly arisen mutations in every generation. Via genetic recombination[iv] some individuals are produced among the progeny that bear so many deleterious

[iv] **Genetic recombination** in Glossary.

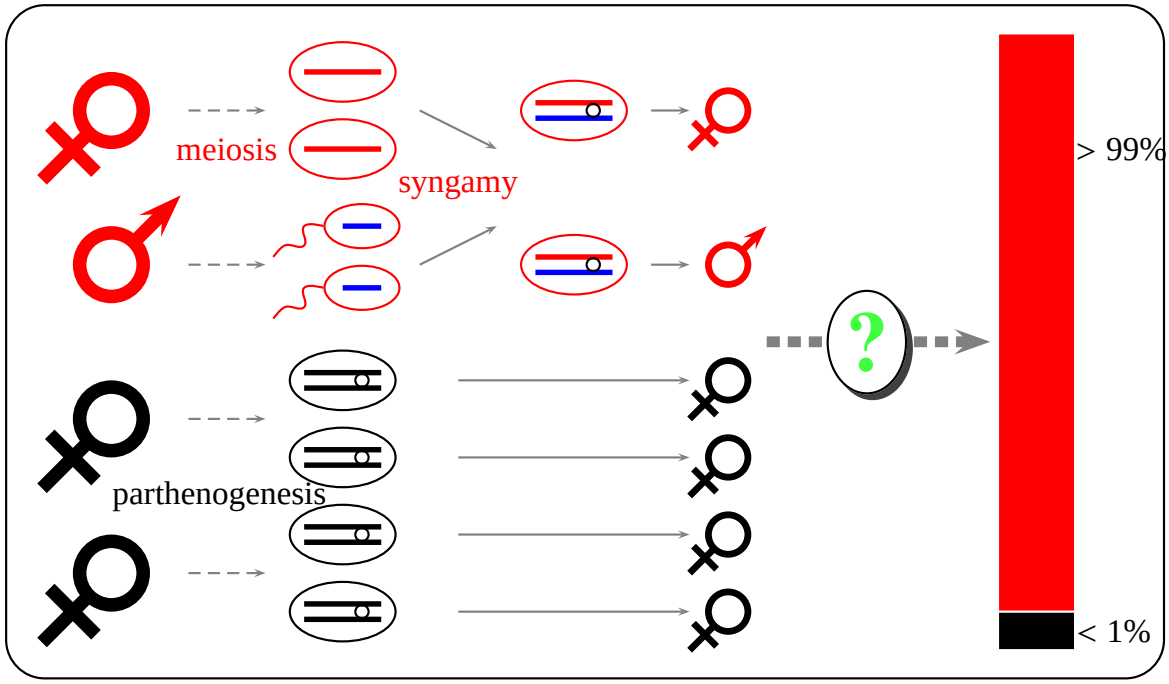



**Figure 1.1.:** This picture demonstrates the paradox of sexuality, with the two fold cost of sex illustrated on the left and the dominance of sexual reproduction in nature on the right. Red color indicates sexual reproduction, while black indicates asexual reproduction. The smaller size of the sperms indicates anisogamy, yet the chromosome in a sperm is of the same size as the chromosome in an egg.

mutations that they are eliminated immediately by selection. Yet some offspring with recombined genomes bear very few deleterious alleles. The operation of the ratchet is, as stated by Bell (1982), straightforward in a haploid[v] population inhabiting a uniform environment. However, the mechanism operates more slowly at any higher degree of ploidy[vi]. The occurrence of epistasis[vii] also will weaken the ratchet mechanism.[viii] Not only its effectiveness depends on the mode of mixis, but also this concept as a whole loses its force (see Bell, 1982, p.103-104).

### 1.2.2 The Red Queen

An immediate fitness benefit of sexual reproduction can be obtained by assuming that the environment varies either in time or in space (Bell, 1982; Maynard Smith, 1971b). A number of authors have argued that biotic factors[ix] are crucial to the evolution of sex. The currently most popular theory, ‘ the Red Queen theory’ (Bell, 1982; Glesener, 1979; Hamilton, 1980; Huston and Law, 1981; Jaenike, 1978; Lively, 2009; Rice, 1983; Van Valen, 1973), states that an or-

v **Haploid** in Glossary.
vi **Ploidy** in Glossary
vii **Epistasis** in Glossary.
viii Compound mutants tend to be less fit than the product of the fitnesses of the single-mutant types. This tendency will make selection for optimal genotypes more effective. As a consequence, the number of compound mutants will be made smaller, and the population will comprise a greater proportion of relatively lightly loaded lines. (Bell, 1982)
ix **Biotic factors**, e.g. predator-prey interaction, host-parasite interaction, intra- or interspecific competition, etc.

ganism's biotic environment tends to be 'contrary'. The advantageous and therefore common genotypes in one generation are disadvantaged in the next generation. Van Valen (1973) named the idea 'the Red Queen hypothesis', since species have to 'run' (evolve) in order to stay in the same place (extant)[x]. Sex and recombination result in progeny genetically distinct from their parents and thus less susceptible to the antagonistic advances made during the previous generations, particularly by their parasites. The Red Queen hypothesis is plausible, as demonstrated by drawing an analogy to the arms race (Ridley, 1993). In evolutionary arms races there is no absolute goal. To escape infection or predation, the species just have to stay ahead of their enemies. In spite of its popularity, the Red Queen hypothesis also has shortcomings. By applying Red Queen models, Howard and Lively (1994) found that parasites generated a decisive advantage to sex only when parasite transmission probabilities were high and the effects of parasite on host fitness were severe, e.g. sterility caused by infection. The theory thus can not be generally applied.

### 1.2.3 Lottery hypothesis

Lottery hypothesis is another approach considering the impact of the environment that varies in time. Williams (1975) presented a number of thought experiments, such as the aphid-rotifer, the elm-oyster, and the strawberry-coral model. In each of these models, a large number of offspring compete for being the winning genotype at a given location. A general characteristic of these models is that the environment of a species is assumed to consist of niches in each of which one winning genotype becomes established, implying that less suitable genotypes become displaced by the best one. Exploring such models in more detail, Maynard Smith (1976) investigated the role of competition among sibling offspring in a system consisting of patches each supporting a single (adult) genotype. In these models the twofold cost of sex could only be counterbalanced if the features of the patch of the sexual offspring were independent of those of the patch of the parent. Maynard Smith (1976) explicitly stated that these results do not match the elm-oyster model (Williams, 1975) that was proposed to explain the advantages of sexual reproduction in species that produce large numbers of offspring. In elm trees, seed dispersal is low and thus most of the seedlings encounter similar environments as their parent trees; in oysters, larval dispersal is high making it unlikely that siblings compete for the same patch. Faced with the unrealistically strong environmental capriciousness required by his sib competition [xi] models in order to explain the evolutionary advantage of sexual reproduction, Maynard Smith (1976) concluded "One is left with the feeling that some essential feature of the situation is being overlooked."

[x] *The most curious part of the thing was, that the trees and the other things round them never changed their places at all: however fast they went, they never seemed to pass anything. "I wonder if all the things move along with us?" thought poor puzzled Alice. And the Queen seemed to guess her thoughts, for she cried, "Faster! Don't try to talk!"* - Lewis Carroll, *Through the Looking-Glass*

[xi] **Sib competition**: competition among siblings

### 1.2.4 The Tangled Bank hypothesis

The Tangled Bank hypothesis has been one of the main theories to explain why most of the organisms reproduce sexually. It was most forcefully defended by Bell, who argued that genetically diverse offspring are able to extract more food from their environment than genetically identical clones. Bell (1982) extended earlier ideas by Williams (1975) and Maynard Smith (1976) on the role of spatial heterogeneity in the maintenance of sexual reproduction. In his seminal book *The masterpiece of nature - The evolution and genetics of sexuality* (1982) he proposed that in contrast to offspring of clonal lineages, sexual offspring compete only partially and thus exploit more resources. This increases the carrying capacity of the habitat. According to Bell, the idea traces back to Ghiselin (1974). However, similar ideas had been proposed much earlier. Dobzhansky (1951, p.1109) argued that "polymorphism[xii] within a species, or any other kind of diversity of sympatric forms, increases the efficiency of the exploitation of the resources of the environment by living matter." A higher level of resource exploitation and therefore of productivity in a sexual population results also from the sib competition processes explored by Maynard Smith (1976). Young (1981) created the notion of 'elbow-room mechanism' to describe the fact that genetic diversity leads to ecological diversity, so that a sexually produced sibship can exploit the environment to a larger extent than a parthenogenetically produced genetically uniform one. Based on more general considerations, Bell (1982) termed this idea 'Tangled Bank' by referring to the concluding paragraph of Darwin's *Origin of species* (1859)

> "It is interesting to contemplate an entangled bank, clothed with many plants of many kinds, with birds singing on the bushes, with various insects flitting about, and with worms crawling through the damp earth, and to reflect that these elaborately constructed forms, so different from each other, and dependent on each other in so complex a manner, have all been produced by laws acting around us."

In order to illustrate the principle that may enable genetically different progeny to extract more food from their environment than genetically identical clones, Ghiselin (1974) and Bell (1982) both used an analogy with economics. In the same way as a new product may increase overall sales by offering an alternative, a new clone or genotype in a spatially heterogeneous environment may exploit unoccupied niches and increase the overall carrying capacity. Since sex creates new genotypes, sexual offspring can occupy additional niches. A diversified brood produced by sexual reproduction may therefore have a greater overall success than a uniform clonal brood. Moreover, since sexual populations occupy many niches, invasion by an asexual clone is hampered. Formal models developed by Bell (1982, p. 132) suggest that in spatially heterogeneous environments asexual populations are unable to drive sexual populations to extinction. Alternatively, Bell (1982) demonstrated that sexual populations can drive asexual populations to extinction, allowing for sampling errors in a finite population. This theory does, however, have limitations similar to those encountered previously by Maynard Smith (1976). Tangled Bank processes may only result in the replacement of asexuals by sexuals if (1) sexual and asexual individuals are completely reproductively isolated, (2) the cost of sex is small, (3) asexuals comprise only few genotypes, (4) competition between genotypes is very limited, and (5) the habitat is very complex.

[xii] **Polymorphic** in Glossary.

Similar results were obtained by other authors that studied mathematical models in which sexual species have a larger niche width than asexual clones. Case and Taper (1986) studied three different versions of such models and concluded that the conditions required for sexual species to stably coexist with or even supplant asexual sister species are high niche differentiation, low environmental variance, and severe resource exploitation. Since usually the asexual clones do not go extinct, these models do not work when there is a continuous formation of new asexual clones. However, using a model based on Lotka-Volterra equations that describe the interaction between two species, Koella (1988) found that the asexual clone can become extinct if population dynamics are not at an equilibrium but show oscillating or chaotic behavior.

Nevertheless, the Tangled Bank hypothesis has been abandoned by many authors due to the limited applicability of mathematical models and a lack of evidence that more sib competition leads to a larger advantage of sexual reproduction. At the moment, the most promoted theory of sexuality is the Red Queen hypothesis that focuses on temporal environmental variation instead of spatial variation.

As argued by Barton (2010), spatial and temporal fluctuations in the environment generate much more fitness variance than can be explained by deleterious mutations. Therefore, we focus in this work on approaches that consider the interaction of species with their environment. Among the above mentioned ecological hypotheses we find the Tangled Bank hypothesis the most plausible. In the next section, it is argued why Tangled Bank is dismissed too early.

## 1.3 Tangled Bank dismissed too early

### 1.3.1 Criticism

The Tangled Bank has been criticized on empirical grounds because the expected effect of a higher density leading to a greater advantage for sexual reproduction could not be confirmed empirically (Ellstrand and Antonovics, 1985; Kelley, 1989). Underlying this conclusion is the idea that the extent of sib competition increases with increasing density and that therefore the advantage of sexual reproduction should also increase with density. Bell abandoned the Tangled Bank hypothesis later in favor of the Red Queen hypothesis, which he always considered as the only plausible alternative to the Tangled Bank (Bell, 1982). The Red Queen hypothesis (Hamilton, 1975; Levin, 1975; Morran *et al.*, 2009) differs from the Tangled Bank hypothesis insofar as it focuses on temporal variation in the environment instead of spatial variation. Bell (1985) confirmed that sex is associated with stable heterogeneous environments, from which he concluded that either the Tangled Bank, the Red Queen, or both are crucial for the maintenance of sex and genetic variation. In a later letter to Nature Burt and Bell (1987) provided evidence against the validity of the Tangled Bank. They compiled data on the recombination frequency in mammals. From the observation that the number of chiasmata[xiii] correlates positively with generation time but not with offspring number, they concluded that recombination functions to combat pathogens rather than to reduce sib competition. Although both the assumptions and the conclusions have been criticized extensively (Charlesworth, 1987; Greenwood, 1987;

[xiii] **Chiasma** in Glossary.

Koella, 1987), Bell appears from then on to have abandoned his belief and interest in the Tangled Bank theory. The theory therefore lost its proponent, resulting in its gradual disappearance from the scientific literature.

### 1.3.2 Ongoing support

Despite of the criticism, a few authors continued to argue in favor of the Tangled Bank hypothesis. Hestmark (1992) found that the frequency of sexual reproduction in a population increases with the intensity of intraspecific competition in a lichen species, as predicted by the Tangled Bank theory. Studying the chiasma frequency in 194 plant species and testing the findings against several hypotheses for recombination, Koella (1993) concluded that sib competition is the only hypothesis that is compatible with the data. He based his conclusion on the fact that the lever of genetic recombination was higher in animal-dispersed than in other species and increased as dispersal distance decreased. A new mathematical model of the Tangled Bank hypotheis was introduced by Gaggiotti (1994), who considered a heterogeneous environment subdivided into patches with different fitness and competition coefficients. In this model, sexual species can resist invasion by asexual clones if they have a competitive advantage in those patches that contribute most to population growth. Doncaster *et al.* (2000) used a Lotka-Volterra competition model based on ecological considerations to show that a sexual species can survive the invasion of an asexual clone due to experiencing a smaller interspecific competition, which is caused by its larger niche width. A different approach was taken by Doebeli (1996), who investigated models that are based on a quantitative trait combined with a fitness function that depends on the density distribution of the phenotypes. The more a phenotype is different from the majority, the higher its fitness. This scenario agrees with the Tangled Bank hypothesis, which favors genotypes that can exploit underutilized resources. Computer simulations of this model show that a sexual population can drive an asexual population to extinction if the asexual population contains only few clones (so that the asexuals cannot exploit all resources), and if random fluctuations are present that can eliminate small populations. It is important to note that due to random mating, the sexual population does not cover all niches, even though it covers a larger range of niches than an asexual clone. Instead, the sexual population changes with time and can thus visit different niche intervals at different times. Recently, Scheu and Drossel (2007) introduced a mathematical model that derives the fitness of the sexual and asexual consumers from the coupled population dynamics of resources and consumers. This model, termed 'structured resource model', is the basis and kernel of this doctoral work. The structured resource model is tailored to annual species with intermittent mixis[xiv], such as aphids or *Daphnia*. It contains a broad spectrum of resources that can be consumed during the season and regrow slowly between seasons. Resources and consumers are specified by two quantitative trait values. Consumers can eat all resources that have a trait value similar to their own. Sexual individuals mate randomly at the end of the season, while asexual clones produce offspring with the same genotype and have the full twofold benefit of a purely female population. Only a limited number of randomly selected eggs give rise to the next generation of consumers (see Section 1.4.1 for more information on the construction of the model). The model thus contains

[xiv] **Intermittent mixis** in Glossary.

stochastic effects, which can drive small asexual clonal populations to extinction. The model includes the repeated invasion of asexual clones by allowing for the offspring of sexual individuals to become asexual with a small probability. When this model is simulated on the computer, it is found that a sexual population can outcompete a set of asexual clones over a wide range of parameter values. Asexual reproduction wins only for high mortality or low resource diversity. In these cases offspring have no advantage from being adapted to resources different from those of their parents. The advantage of the sexual population thus lies again in the fact that it can produce offspring that exploit underutilized resources. Similar to the model by Doebeli, random mating limits the niche width of the sexual population, which covers only part of the resources. Concordantly, the mean trait value of the sexual population changes as the population moves to other resources over the course of time (see Chapter 2 for a graphical demonstration).

It is instructive to compare the model by Scheu and Drossel (2007) to the one by Maynard Smith (1976). The main mathematical difference consists in the fact that the resources are generated at random in each generation in the model by Maynard Smith, while they have explicit dynamics and regrow slowly after consumption in the model by Scheu and Drossel (2007). The latter model includes a negative correlation between resource use in the previous generation and resource availability in the current generation. Furthermore, the interpretation of the two models is different: in the model by Maynard Smith, each 'patch' can have one winning genotype, assuming that each patch represents one niche and that offspring must disperse far in order to be able to cover all patches. In the model by Scheu and Drossel (2007), the different niches are assumed to be present within a single patch, which means that offspring that remain close to their parents can nevertheless use different resources. This can be considered as the main difference between the Tangled Bank and the lottery concept.

Another strength of the model by Scheu and Drossel (2007) is that it includes the repeated invasion of asexual clones and thus demonstrates that the prevalence of sexual reproduction can be an equilibrium state in spite of continued exposure to asexual invaders. Previous models have merely considered the maintenance of sexual reproduction in the presence of one or very few asexual clones, and even fewer models have included mechanisms that lead to the extinction of asexual clones. However, the extinction of asexual clones is a prerequisite for the maintenance of sexual reproduction if new asexual clones can arise.

### 1.3.3 Higher population density does not imply a larger advantage to sexual reproduction

The Tangled Bank theory that focuses on the role of spatial heterogeneity at maintaining sexual reproduction, as argued above, have been dismissed too early. The last two models (Doebeli, 1996; Scheu and Drossel, 2007) show that the frequent assumption that the Tangled Bank hypothesis implies a larger advantage of sexual reproduction when the population density is larger is not justified. Therefore, the Tangled Bank hypothesis should not be rejected in consequence of the lack of empirical evidence for a density dependent advantage of sexual reproduction. In the model by Doebeli (1996), the population size is determined by the carrying capacity, and the trait distribution is determined by the fitness function combined with random mating. This means that the range of resources that can be exploited is not determined by the population

density, and that the advantage of sexual reproduction does not increase with increasing population density. This situation is even more pronounced in the structured resources model (Scheu and Drossel, 2007), where a larger population size (implemented by allowing a larger number of coexisting genotypes) implies a smaller advantage for sexual reproduction. The reason is that sexual reproduction is advantageous only if there is a sufficient amount of underutilized resources. If fewer genotypes are allowed to coexist, there are more underutilized resources for the sexually produced offspring to exploit. In contrast, if a set of asexual clones can cover a large part of the resources, asexual reproduction wins over sexual reproduction. These models also show that the advantage of sexual reproduction according to the Tangled Bank theory does not lie primarily in the reduction of sib competition. Rather, it lies in the fact that offspring are different from the parents. This means that the model reduces the negative effect that resource exploitation by the parents has on their offspring. Again, this means that the litter size or the population size is of little relevance for this advantage and that the empirical data cited by Burt and Bell (1987) do not justify rejection of the Tangled Bank hypothesis.

All these considerations show that the Tangled Bank hypothesis, rather than being dismissed, should be extended such that it also includes temporal variation. This temporal variation is due to the fact that sexual offspring are able to exploit resources that have not been used by their parents. Such underutilized resources exist when locally only a fraction of those genotypes of the population is present that would be required to fully exploit all resources.

### 1.3.4 Three overlooked points in interpreting the Tangled Bank

The two models by Doebeli (1996) and Scheu and Drossel (2007) shed new light on the Tangled Bank theory and contribute concepts and ideas that have been neglected so far. By extending and modifying the structured resource model (Scheu and Drossel, 2007), we fairly defend the Tangled Bank theory and demonstrate its general validity in this work. In the light of the structured resource model successfully explaining the maintenance of sex, we claim that the lack of acceptance of the theory is due to conceptual deficits. In the following, we argue that three important aspects of the interaction of a population with a heterogeneous environment have been neglected so far: (1) the essential role of resource availability at determining the mode of reproduction; (2) the fundamental distinction between the influence resources including abiotic and biotic factors that affect population dynamics in a density dependent way (Begon *et al.*, 2005), and the influence of abiotic physicochemical conditions that affect population dynamics in a density independent way; and (3) a local negative feedback between resource consumption and resource availability, leading to temporal changes in resource usage, which in fact introduces features of the Red Queen concept into the Tangled Bank theory. Including these three overlooked points, the structured resource model shows a great potential of explaining the evolution of sexuality in the Tangled Bank theory.

#### Resources as drivers of the mode of reproduction

The importance of resources at explaining sexual reproduction was stressed decades ago by Ghiselin (1974). Glesener and Tilman (1978) also observed that sexual reproduction appears

to be related to tight biotic coupling. Bell (1982, 1988) and many others stressed repeatedly the general observation that the initiation of sexual reproduction coincides with the depletion of resources (Hebert *et al.*, 1988). In spite of these observations, nobody formalized these ideas by using mathematical models that explicitly include the coupled dynamics of sexual and asexual consumers and their resources, or the onset of sexual reproduction when resources become scarce. This was done for the first time in the structured resources model by Scheu and Drossel (2007).

By focusing on the fundamental role of resources, the structured resource model encompasses a wider spectrum of interactions than the Red Queen model. While the Red Queen model requires a tight interaction between two species, the structured resources model is based on consumers that interact with several resources, which may include dead organic matter (for decomposers) or mineral nutrients (for microorganisms and plants). Included are all resources that potentially limit population growth because they are renewed slowly (Hairston *et al.*, 1960). Slow renewal is typical for many resources: prey and plants need time to regrow, and minerals are replenished by chemical weathering or the mineralization of dead organisms.

The genetic basis of ecological traits that determine resource use is certainly complex and includes a high potential for rapid adaptation, as is evident from the frequent occurrence of adaptive radiation[xv]. For this reason, the structured resources model does not rely on a specific genetic architecture, but includes the potential for exploiting new resources in a simple quantitative genetic way (see Chapter 2). The validity of the structured resource model is actually independent of genetic implementation. In Chapter 3, we explicitly model the genetics in the framework of the structured resource model. There, we also test the validity of the model with two additional genetic implementations.

### Distinction between abiotic and biotic factors, and geographic parthenogenesis

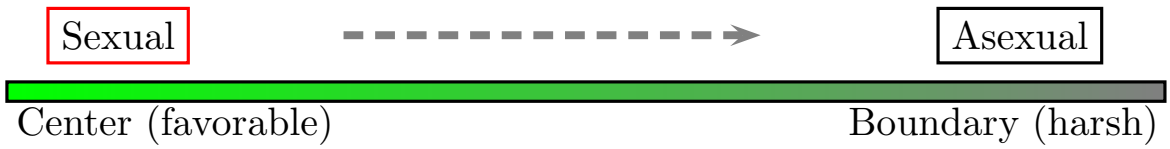



**Figure 1.2.:** Illustration of geographic parthenogenesis. As the environment conditions change over from favorable to harsh, e.g. from the south to the north or from low to high latitude, the dominant mode of reproduction switches over from sex to parthenogenesis Vandel (1928).

Often, considerations about the success and limitation of the Tangled Bank theory for explaining sexual reproduction were based on the niche concept (Bell, 1982; Maynard Smith, 1971b). The performance of species along environmental gradients was discussed without distinguishing between factors affecting species in a density dependent and a density independent way. This leads to the riddle of why parthenogenetic rather than sexual species appear to benefit from environmental harshness. Sexual populations prevail in favorable environments, while asexual populations prevail in harsh, unpredictable, disturbed, and novel environments, such as at high as compared to low latitudes, at high as compared to low elevation, and in deserts as

[xv] **Adaptive radiation** in Glossary.

compared to moist regions (Bell, 1982; Kearney, 2003) (Fig. 1.2). This phenomenon is called geographic parthenogenesis (Vandel, 1928). The riddle can be solved when realizing the fundamental distinction between physicochemical conditions and resources, as demonstrated in Chapter 2, 3, and 5. Habitats need to be distinguished according to the predominance of factors responsible for population dynamics, as emphasized by DeAngelis and Waterhouse (1987) and Krebs (2008). Already Bell (1982) emphasized that geographic parthenogenesis must be due to the fact that competition and crowding, which elicit sex, are not important in harsh environments, where mortality due to abiotic factors is high. Or, as expressed by Hestmark (1992), "sex, by generating genetic variation, represents an escape from competition in biologically saturated environments." In harsh environments, the carrying capacity of the resources is never reached, the advantage of sex is barely expressed, and the winning mode of reproduction is parthenogenesis.

These intuitive ideas about the capability of the Tangled Bank hypothesis to explain geographic parthenogenesis are confirmed and implemented mathematically in this work.

## Tangled Bank includes Red Queen

Another riddle of the Tangled Bank is why sexual species continue to produce sexual offspring even in species that are poor dispersers. As outlined by Maynard Smith (1976), sib competition processes are poor at explaining the maintenance of sex at the locality of the parents, since local environmental conditions are unlikely to vary strongly from generation to generation. If the 'local environmental conditions' mentioned by him (and others later; see Bell (1982)) are understood as 'local physicochemical conditions', this assumption is certainly valid. Offspring are very likely to encounter similar climatic and structural habitat conditions as their parents. However, what has been neglected is that the resources used by their parents are likely to be depleted and the resulting modified resource distribution confronts the offspring with a new biotic condition. This effect is most pronounced at the locality where the parents resided and reproduced. Locally resource exploitation by parents negatively correlates with resource availability to offspring that are genetically similar and therefore rely on similar resources. This negative correlation provides exactly the mechanism necessary for the maintenance of sexual reproduction, and is included in the structured resource model. It leads to a negative correlation between the fitness of a given genotype in the parent and offspring generations. This is the essence of the Red Queen model, but has been overlooked as a part of sib competition models. In fact, the negative correlation and the potential for explaining sexual reproduction can be stronger in resource based models than in models based on host-parasite interactions, as resources form the essential prerequisite for any organisms to survive and reproduce. To include a resource based feedback into the fitness of a genotype actually means to introduce a Red Queen mechanism into the Tangled Bank theory, suggesting that both may be seen as part of one unified theory. This has already been pointed out by Doebeli (1996), who implemented the Tangled Bank concept such that rare genotypes have a higher fitness than common genotypes, leading to a Red Queen like evolution of the genotype distribution. In Chapter 2, this effect is emphasized in the context of the structured resource model, where the temporal fluctuation of the resource usage of the population is investigated.

## 1.4 Reconsideration of the Tangled Bank hypothesis

This work consists of two parts that aim to prove the validity of the Tangled Bank theory. The first part deals with the advantage of sexual reproduction of short-lived organisms, while the second part deals with long-lived organisms. The approaches used in the work are based on the structured resource model. Therefore, this section begins with a brief description of its construction, and proceeds with the its modifications and the intensions of the two parts of the work.

### 1.4.1 The structured resource model by Scheu and Drossel

Due to the global extinction crisis, the relation between community characteristics and species diversity found considerable interest in recent years (Balvanera *et al.*, 2006; Naeem *et al.*, 2009). It is increasingly recognized that species diversity within communities and genotype diversity within species are of similar importance for ecological processes (Hughes *et al.*, 2008; Roman and Darling, 2007). The structured resource model (Scheu and Drossel, 2007) is based on the diversity of species' resources. The model contains diverse resources that have limited maximum biomass and regrow slowly. In the model, resources are arranged in a two-dimensional trait space with trait values ranging from 1 to $L$ in both dimensions. For $L = 20$ there are 400 different types of resources. The trait space of the consumers is also two-dimensional and is scaled such that the resource that can be consumed best is the one that has the same trait values as the consumer (Fig. 1.3). Therefore, the consumer trait values also range from 1 to $L$ in both dimensions. There are as many possible consumer genotypes as resource types. The dynamics of resource and consumer populations is divided into two stages. First, there is the stage of rapid asexual consumer growth and fast resource consumption, until consumer growth rates become negative because resources become depleted. Second, there is the stage of egg production and selection. Sexual consumers mate and lay eggs via recombination, while asexual consumers lay eggs that are genetically identical to their parents. With a small probability a sexual egg can become asexual, thus asexual invaders are continuously introduced to the sexual population. A few offspring genotypes that start the growing cycle in the next season are randomly selected, while parent individuals are removed as the model is tailored to annual species. Resources recover partially until the beginning of the next season.

The model uses quantitative genetics, a theory concerned with characters controlled by large number of genes. Already Mendel had noticed in his original paper in 1865 that characters influenced by many genes can generate a continuous frequency distribution. (Ridley, 2004, p.226-227) According to the theory of quantitative genetics, a character influenced by a large enough number of genes will have a normal frequency distribution. The structured resource model, in this case, focuses on the character that determines the resource exploitation of the individual. The genotype of a sexual offspring is thereby randomly chosen from a Gaussian distribution around the midparent value.

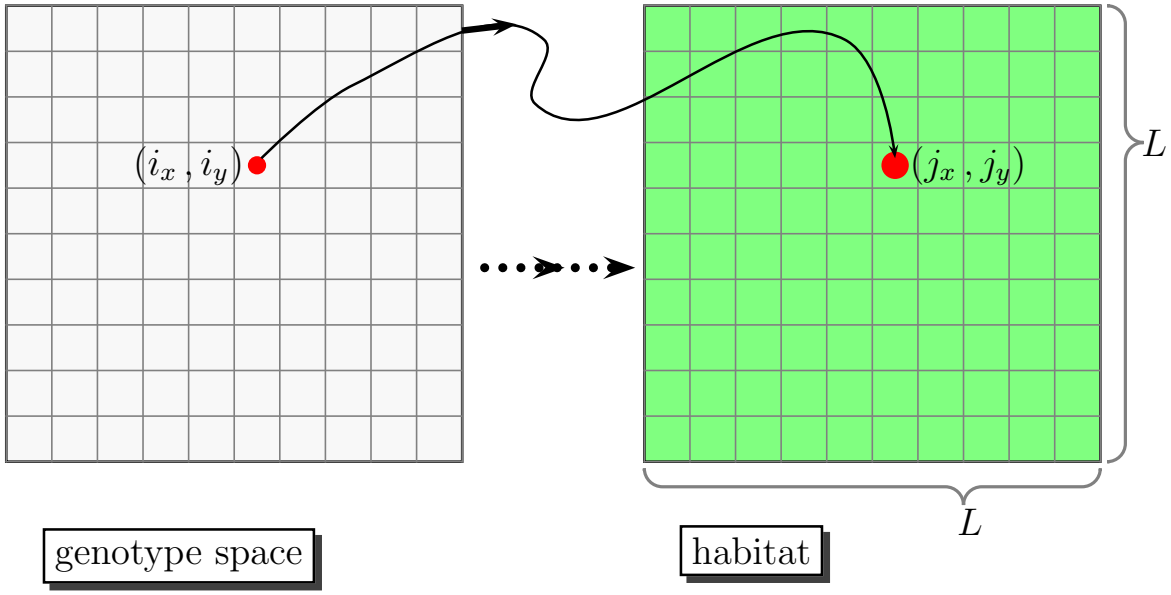



**Figure 1.3.:** Illustration of the structured resource model. On the right-hand side is the two-dimensional array of resource niches of the size $L \times L$. On the left-hand side is the corresponding genotype space with equal number of genotypes. A consumer with genotype $(i_x, i_y)$ is best adapted to the resource with the trait values $(j_x, j_y)$ if $(i_x, i_y)$ and $(j_x, j_y)$ are identical. The consumer can also exploit other resources, but less efficiently.

### 1.4.2 The modified models and geographic parthenogenesis in short-lived organisms

In Chapter 2, we show the great potential of the Tangled Bank theory by a model based on the structured resource model. The model differs from the original structured resource model (Scheu and Drossel, 2007) by including a spatial dimension and by making the patches different from each other, which is reminiscent of the model by Ament *et al.* (2008). Thereby, we demonstrate that the structured resource model covers all the three overlooked points mentioned in Section 1.3.4. First, the model considers the important role of resources at determining the mode of reproduction by focusing on the traits that determine the exploitation of resources. Second, the riddle of the geographic parthenogenesis can be solved by distinguishing density dependent from density independent variables. While a density independent mortality increases along the spatial dimension, the dominant mode of reproduction switches over from sexual to asexual (Fig. 1.2). Third, by monitoring the temporal resource use we show that the interaction with resources connects the Tangled Bank and Red Queen Hypotheses. The ever changing mean trait value in a sexual population present an escape from the resource scarceness caused by the parent generation, which is similar to the escape from the parasite that is adapted to the common genotype in the previous generation.

Moreover, by making the resources different from patch to patch we include the disadvantage of sexual reproduction breaking up adaptations in the model. Thereby a third additional trait that varies from patch to patch is introduced for the resources. A sexual offspring may be assigned

with a trait value that differs from that of the local resources. Yet, this modification can also be beneficial for sexual populations in case of numerous migrating events between the patches.

Concerning the complexity of the genetic basis underlying the ecological traits that determine resource exploitation, the validity of the model shall not depend on a special genetic architecture. In Chapter 3, we first examine the validity of the structured resource model using explicit genetics instead of quantitative genetics, and then briefly test the model with two more different genetic implementations. Here, we again include a spatial extension of many patches of structured resources, and thereby reproduce the phenomenon of geographic parthenogenesis. Thus, structured resource model inspired by the Tangled Bank hypothesis is generally valid as long as its assumptions are guaranteed, i.e., resources are so diverse that there are always unexploited resources, each resource is limited so that a finite carrying capacity is defined, and exploited resources are slowly recovered so that progeny relying on the same resources are disadvantaged. To drive the asexual clones to become extinct the model must also include stochastic effects, such as genetic drift[xvi].

Using explicit genetics, we also include the increase of mutation rate that is often stimulated by increasing environmental stress (Baer, 2007; Goho and Bell, 2000). Each locus can undergo a mutation. By means of such mutations asexual population can also gain new niches. In Chapter 3, we compare the dynamics of genetic diversity in sexual populations with that in asexual populations, and analyze the advantage of sexual reproduction in greater depth. To clarify the impact of structured resources, we perform a simulation of a null model without resources, and show that the genetic diversity merely under the operation of genetic drift quickly declines both in asexual and sexual populations. A heterogeneous environment, therefore, is vital for the genetic diversity among species.

In both chapters, the patches along the spatial dimension are connected by migration between neighboring patches. The influence of migration on the geographic distribution of sexual reproduction is sophisticated. As shown in the corresponding sections (Section 2.3.2 and 3.3.2), depending on the migration rate migration can either advantage or disadvantage sexual reproduction.

So far, the models are all tailored to short-lived species that reproduce only once per life time. The validity of the structured resource model, and the Tangled Bank hypothesis, has not been proven for long-lived species. Actually, before this work there is no mathematical model that explicitly examines the advantage of sexual reproduction of long-lived species that reproduce more than once per life time. Such a model must include an age structured population, and thus involves the field of life history theory (see below). Studies that aim at explaining sexual reproduction for long-lived species demand a synthesis of the theory of sex and the theory of life histories.

### 1.4.3 The structured resource model of long-lived organisms

After the general validity of the Tangled Bank is proven for short-lived organisms, we further apply it to long-lived organisms. Before this work there is no established model of an age structured population that can be easily put into the framework of the structured resource model.

[xvi] **Genetic drift** in Glossary.

Therefore, we construct a mathematical model that explicitly simulates the interaction between long-lived organisms and their resources. In order to understand this new element of our model in more details, we first discuss the life history traits under the influence of limited resources in Chapter 4. We then embed this minimal life history model into the structured resource model in order to investigate the advantage of sex.

## A brief introduction to the life history theory

"Life histories lie at the heart of biology; ... Fascinating in themselves, life histories are also the keys to understanding related fields." (Stearns, 1992) The theory of sex is the related field in our case. Life history theory, as termed, explains essential features of a life cycle. The important life history traits that characterize a life cycle are:

Size at birth
Growth pattern
Age at maturity
Size at maturity
Number, size, and sex ratio of offspring
Age- and size-specific reproductive investments
Age- and size-specific mortality schedules
Length of life

as listed in Stearns (1992).

Life history traits are shaped by natural selection, and are optimized during evolution. Classical approaches to life history theory are optimizations. Traditionally, the life history traits are postulated, e.g. in Roff (2007, Box 1) the growth pattern, the number of offspring of a female in age class $X$, and the probability that a newborn individual survives at least to beginning of age class $X$ are specified for ectothermic vertebrates. These traits are connected by trade-offs, e.g. trade-off between reproduction and survival, and trade-off between current reproduction and future reproduction. Based on the trade-offs the fitness is maximized to determine an optimal life cycle.

In life history theory fitness is measured by the maximum growth rate $r$. The central equation used to determine the maximum growth rate is the Euler-Lotka equation (Euler, 1760; Lotka, 1907),

$$\sum_X e^{-rX} l(X) m(X) = 1^{\text{xvii}},$$

where $X$ denotes the age class. $l(X)$ is the probability that a newborn individual survives at least to beginning of age class $X$, and $m(X)$ is the average number of offspring of a female in age class $X$. A population that does not change in size is thus in stationary age distribution (see Section 4.1). In a stationary population the number of reproducing daughters expected per female per life time is 1, since it is the per-generation rate of multiplication of a population.

The Euler-Lotka equation is no doubt elegant. Yet it is not directly applicable in our model, since there is no explicit connection to resource dynamics. In this work we make a different

[xvii] For derivation see Stearns (1992, p.24)

approach to life history. In our model life history traits such as growth pattern and age at maturity can be derived from the interaction with limited resources, given the body mass at birth and at maturity. Growth is an important part of life cycle. As defined by Von Bertalanffy (1938): "Growth is the measurable increase of an organic system, produced by its assimilation of materials obtained from its environment." Therefore, we perform a minimal consumer-resource system, and investigate the interaction between the population dynamics and the dynamics of the limited resources in its environment. The resources $R$ grow according to the logistic function (see the footnote on page iii). The resource exploitation of consumers and their metabolism[xviii] are scaled with individual body mass of the consumers.

## Metabolic theory

For scaling with body mass we use metabolic theory. It has been know since early in the 20th century (Brown *et al.*, 2004) that all characteristics of an organisms scale with body mass. J. Huxley (1932) pointed out that the corresponding relationship can be described by power functions of the form

$$Y = Y_0 M^b \,,$$

where $Y$ represents any characteristics, e.g. metabolic rate, $M$ represents the body mass, $Y_0$ is a normalization constant, and $b$ is an allometric exponent. Based on Euclidean geometric scaling, the allometric exponent should be $2/3$, i.e., surface divided by volume. Yet, the metabolic rate[xix], $I$, scales as

$$I = I_0 M^{3/4} \,,$$

according to Kleiber's law (Kleiber, 1932). Here, $I_0$ is a mass-independent normalization constant. G. West *et al.* (1997, 1999a,b) showed that this quarter-power allometric scaling could be explained by the fractal-like designs of surfaces and networks that determine the rate of resource assimilation and the rate of energy allocation.

Based on the allometric scaling alone, Chapter 4 explains three interesting issues in life history: (1) in a population that is constrained in size $K$-strategy prevails over $r$ strategy[xx] (Pianka, 1970); (2) the body mass of a certain lineage increases over evolutionary time (Cope's rule (Hone and Benton, 2005)); and (3) in a population of individuals that mature later the expected life time is longer. The common cause of these issues is that an individual with larger body mass requires less energy per mass, according to the metabolic theory. Therefore, large body mass is preferred in this minimal model that is solely based on the metabolic theory.

## A more significant advantage of sexual reproduction of long-lived species

The advantage of sexual reproduction has not been mathematically investigated for long-lived organisms before this work. The absence of asexual forms in mammals and birds is explained

[xviii] **Metabolism** in Glossary.
[xix] **Metabolic rate** in Glossary.
[xx] $K$-**strategy** and $r$-**strategy** in Glossary.

from the genetic aspect. It has been claimed that genomic imprinting[xxi] is a vital mechanism for a sexual organism. An embryo can not fully develop without a male germ line (Swales and Spears, 2005). From the ecological point of view the reason for the absence of parthenogenesis in mammals is still unclarified.

In Chapter 5, we modify the structured resource model in order to explain the maintenance of sex and geographic parthenogenesis for long-lived organisms. Here, we introduced two variables to the model: the minimum adult body mass and the maximum consumption rate that are considered as constants in the model of short-lived organisms. The minimum adult body mass determines the age at maturity, when all other parameters are kept the same. This variable has an interesting impact on the advantage of sexual reproduction. If the minimum adult body mass is too small, the twofold cost of sex is frequently operated, so that sexual populations are largely disadvantaged. If the minimum adult body mass is too large, sexual populations equally suffer from resource scarceness as asexual populations, since no genetically different offspring are born for a long period. Therefore, only intermediate adult body mass is beneficial for sexual reproduction.

With the model of long-lived organisms we also perform simulations with extremely high population density. In contrast to the case of short-lived organisms, sexual reproduction still dominates even when a great part of all the niches in the patch is occupied. The advantage of sexual reproduction is larger in long-lived organisms than in short-lived organisms. Here, the parents can exist with their offspring in the same time interval, and thus directly compete with the offspring for resources. The disadvantage of asexual populations is now more severe in case of resource scarceness. Asexual newborn offspring that rely on the same resources as the resources of their parents grow much more slowly than the sexuals, since they do not only compete with their siblings but also their parents. In this model, the death rate is also related to the body mass by allometric scaling, $p \sim B^{-3/4}$. The slowly growing asexual individuals, therefore, have a higher death rate than the sexuals in the same age class. In this case, producing more offspring brings no benefit to the asexuals. The advantage of sexual reproduction is more significant in long-lived species.

With all the effort we put in this work, the Tangled Bank is proven to be a general theory of sex. The theory explains not only the predominance of sexual reproduction but also the phenomenon of geographic parthenogenesis. With the structured resource model (Scheu and Drossel, 2007) of the Tangled Bank, a pattern resembling geographic parthenogenesis is reproduced (see Chapter 2). The results are independent of genetic implementations (see Chapter 3). Moreover, the theory holds not only for short-lived organisms but also for long-lived organisms (see Chapter 5). The advantage of sex in long-lived organisms is even larger according to this mathematical model of the Tangled Bank theory. The theory, therefore, may even explain the absence of parthenogenesis in mammals and birds from the ecological aspect. Throughout the work, it is shown that the Tangled Bank actually includes the Red Queen mechanisms and puts it in a wider context. As Red Queen is the popular theory of sexual reproduction in this field, Tangled Bank shall not be dismissed but reconsidered as one of the main theories to explain why most of the living organisms reproduce sexually.

[xxi] **Genomic imprinting** in Glossary.

# Part I.
# Short-lived organisms

# 2 Temporal patterns of resource usage in an ecological model for sexual reproduction and geographic parthenogenesis

The phenomenon of geographic parthenogenesis is closely tied to the question of why sexual reproduction is the dominant mode of reproduction in animals and plants. Geographic parthenogenesis describes the fact that many species reproduce asexually at the boundaries of their range. In this chapter, a mathematical model that derives the dominance of sexuals at the center and the dominance of asexuals at the boundary of a species' range from exactly the same mechanism is presented. The model is tailored to annual species with intermittent mixis and low survival of offspring, such as *Daphnia* and aphids. The model adopts the structured resource model (Scheu and Drossel, 2007) of a single patch, and adds a spatial extension to the original model. Several patches of resources are arranged in a row, with a gradient of those parameters that typically vary through the range of species. By letting sexually and asexually reproducing populations compete, the typical pattern of geographic parthenogenesis is obtained.

In light of the framework of the model two major questions are addressed in this chapter: How are the prevalence of sexual reproduction and the phenomenon of geographic parthenogenesis related to resource availability? What is the pattern in space of resource and consumer dynamics? Thereby, the continuously changing resource usage of the sexual population is investigated. It is demonstrated that the temporal change of resource usage and therefore the advantage of sexuality is most significant at the center of a species' range.

## 2.1 Geographic parthenogenesis and its explanations

Any theory that aims at explaining why sexual reproduction prevails in most organisms, must be in agreement with the general patterns of parthenogenesis, in particular geographic parthenogenesis. Geographic parthenogenesis describes the fact that many species reproduce asexually at the boundaries of their range, i.e. in northern regions, at high elevations, or at the transition to deserts, while they reproduce sexually closer to the center of their range (Bell, 1982; Glesener and Tilman, 1978; Hebert *et al.*, 1988; Vandel, 1928). A few examples are listed in Table 2.1.

For both phenomena, sexual reproduction and geographic parthenogenesis, exist a variety of explanations and models, however, these cannot easily be linked.

Theories for sexual reproduction (see Chapter 1 for more information) argue that it can purge the genome more efficiently from deleterious mutations under appropriate conditions (Charlesworth, 1987; Morran *et al.*, 2009; Muller, 1932), and that it facilitates adaptation to a novel environment when sex leads to an increased variance in fitness (Morran *et al.*, 2009). A variation of the latter hypothesis, when the environment of a species is dominated by the negative influence of another species, is the Red Queen hypothesis (Hamilton, 1980; Lively and Dybdahl, 2000; Lively, 2009; Van Valen, 1973). Furthermore, sex can restore genetic combinations that become lost due to drift but that are favored in temporally or spatially fluctuating environments (Otto and Lenormand, 2002). In particular, environmental heterogeneity facilitates sexual reproduction, as stated in the Tangled Bank hypothesis (Bell, 1982), and as

**Table 2.1.:** Examples of geographic parthenogenesis listed taxonomically; modified from Glesener and Tilman (1978).

| **Taxon** | **Species** | **Geographic distribution** | |
|---|---|---|---|
| | | **sexual reproduction** | **parthenogenesis** |
| Acari | ixodid tick *Haemaphysalis longicornis* | southern Japan and Korea | northern Japan and the USSR (Hoogstraal *et al.*, 1968) |
| Diplopoda | millipedes *Isobates varicornis* and *Archiboreioulus pallidus* | central Europe (Schubart, 1934) | Finland (Palmén, 1949) |
| Isopoda | wood louse *Nagara modesta* | Java, Sumatra, and Saleyer | Christmas Island (Hill, 1948) |
| Insecta.-Embioptera | *Haploembia solieri* | Mediterranean mainland in Europe | islands off the cosast of Italy (Stefani, 1956) |
| Orthoptera | *Poecilimon intermedius* (Tettigoniidae) | Mediterranean region (White, 1973) | Siberia and the central Asian highlands (Bei-Bienko, 1954) |
| Phasmida (Cheleutoptera) | *Bacillus rossius* | southern Italy and north Africa (Pijnacker, 1969) | France and northwestern Italy |
| Hemiptera | *Phenacaspis pinifoliae* (Diaspididae) | central and southern California | northern California, Arizona, and Utah (Brown, 1965) |

confirmed by a recent experimental study (Becks and Agrawal, 2010). Natural environments are usually heterogeneous, as demonstrated by experiments that show that genetically diverse populations can better exploit resources than genetically homogeneous populations (Doncaster *et al.*, 2000). Generally, it is increasingly recognized that genetic diversity affects the performance of communities in various ways including e.g., competition for resources and community productivity (Hughes *et al.*, 2008).

Theories for geographic parthenogenesis propose that parthenogenesis is a side effect of hybridization[i] in boundary regions (Kearney, 2005) or of selection for polyploidy[ii] (Otto and Whitton, 2000). Other authors emphasize that asexuals are capable of colonizing new habitats faster (Cuellar, 1997; Law and Crespi, 2002) or that asexual reproduction arises whenever environmental changes may have provided opportunities, e.g., climatic oscillations of the Pleistocene, for shifts to asexuality (Hörandl, 2009a). In the only spatially extended mathematical model for geographic parthenogenesis that exists so far, Peck *et al.* (1998) explicitly showed that a sufficiently strong source-sink effect[iii] can lead to a dominance of parthenogenetic reproduction in boundary regions, because sexuals cannot establish the phenotype that is optimal for this region. In this model, asexuals are assigned a lower fitness than sexuals, given the same degree of adaptation to their environment, which changes along the spatial gradient. The fitness of the sexuals in the boundary region is even lower than that of the asexuals because of the inflow of maladapted genotypes due to migration (Peck *et al.*, 1998). The immigrating sexual individuals mate with the local sexual population and thus prevent it from becoming adapted to the local environment. In contrast, the local asexual genotypes can be perfectly adapted to the environment. An alternative scenario is envisaged by Gaggiotti (1994) who has pointed out that geographic parthenogenesis could occur as an equilibrium phenomenon if parthenogenetic reproduction was selectively favored against sexual reproduction in the boundary regions, while sexual reproduction was favored elsewhere.

The latter idea, that the mode of reproduction prevailing at a certain location should be the one that has a selective advantage at this location, has been most forcefully put forward by Bell (1982), and it is justified by the observation that many organisms have the ability to switch between different modes of reproduction. In particular, situations of crowding and starvation elicit sexuality in organisms that reproduce asexually at other times. Because of this observation, it is legitimate to assume furthermore that resource availability is the main determinant of the fitness of an individual. Indeed, Glesener and Tilman (1978), citing the book of Ghiselin (1974), pointed out that the depletion of resources favors those individuals that switch to a currently underutilized resource. Thus, sexual reproduction should be favored in heterogeneous environments with a broad spectrum of resources that have a limited availability, while parthenogenetic reproduction should prevail where the resource limitation is not important or affects both modes of reproduction in the same way, as is the case in new habitats or in habitats with high mortality or small resource richness. This is the essence of the argument put forward in Bell (1982).

---

[i] **Hybridization** in Glossary.

[ii] **Polyploidy** in Glossary.

[iii] **Source-sink effect**: "(...) a local demographic surplus arises in good quality habitats (source), and a local demographic deficit occurs in habitats of poor quality (sink). Within a landscape, a permanent migration of propagules or individuals from source to sink habitats may lead to a stabilization of the overall demographic system." (Dias, 1996)

However, older mathematical implementations of the Tangled Bank hypothesis (Case and Taper, 1986) that include a broad spectrum of resources result in the coexistence of both modes of reproduction and can neither tolerate a continuous creation of new asexual clones, nor do they lead to the phenomenon of geographic parthenogenesis. The Tangled Bank hypothesis was also rejected due to the lack of empirical evidence. When interpreted as predicting a greater advantage to sexual reproduction when numbers of offspring and thus sibling competition is larger, it does not agree with empirical investigations (Ellstrand and Antonovics, 1985; Kelley, 1989). Burt and Bell (1987) rejected the Tangled Bank hypothesis on similar grounds, as mammal species that have more offspring do not have increased rates of recombination. However, these arguments have been questioned by other authors (Charlesworth, 1987; Greenwood, 1987; Koella, 1987).

A different approach to the mathematical modelling of ideas related to the Tangled Bank hypothesis was taken by Scheu and Drossel (2007), where the number of locally coexisting genotypes was limited and drift was assigned an important role. The model is tailored to *r*-strategists with intermittent mixis and explicitly includes the interaction of the consumers with their resources. Resources are structured, and one consumer genotype therefore can only exploit a small part of the resources. Similar to older Tangled Bank models, it relies on quantitative genetics with a fixed genetic variance of sexuals. Slow regrowth of resources combined with stochastic effects due to restrictions on the number of locally coexisting genotypes, leads to the prevalence of sexual reproduction in spite of the cost of producing males. Interestingly, in this model the advantage of sexual reproduction does not increase with increasing density, since this would decrease the stochastic effects that result in different resources being exploited at different times. The result of prevalence of sexual reproduction holds for a wide range of parameters (Ament *et al.*, 2008; Scheu and Drossel, 2007). However, with increasing mortality or decreasing resource richness, the dominant mode of reproduction becomes asexual. This finding suggests that the model can be used to generate a scenario that shows geographic parthenogenesis.

In this chapter, a modified model based on the one by Scheu and Drossel (2007) is investigated. The modified model includes a spatial dimension, in order to generate a setup that can show geographic parthenogenesis. Alongside the spatial dimension, a new component is added to the consumer genotype. This new component characterizes the adaptation to the local environment. With the additional dimension of the genotype, the modified model stresses the disadvantage of sexual reproduction that breaks up well adapted genotypes. By arranging patches of resources along a habitat that stretches from regions of low consumer mortality to regions of high consumer mortality or from regions of high resource diversity to regions of low resource diversity, a pattern resembling the phenomenon of geographic parthenogenesis is revealed. The model thus shows that the dominance of sexuals at the center and the dominance of asexuals at the boundary of a species' range can be explained by exactly the same mechanism, i.e., the interaction with resources.

In framework of this model with the quantitative genetic approach, we investigate the mechanisms responsible for the prevalence of sexual reproduction. Thereby, we illustrate the spatial and temporal dynamics in resource use. We show that the advantage of sexual reproduction is largest when the benefit of switching to unused resources is high and when mortality is low. This

insight suggests that in structured resource space low mortality supports genotype diversity, the most pertinently acknowledged advantage of sexual reproduction.

In the next section, the model will be defined in more detail. After that, results of computer simulations will be presented with explanations of how they follow from the rules of the model. At the end of the chapter, there will be a discussion where the results are placed in a wider context.

## 2.2 Model

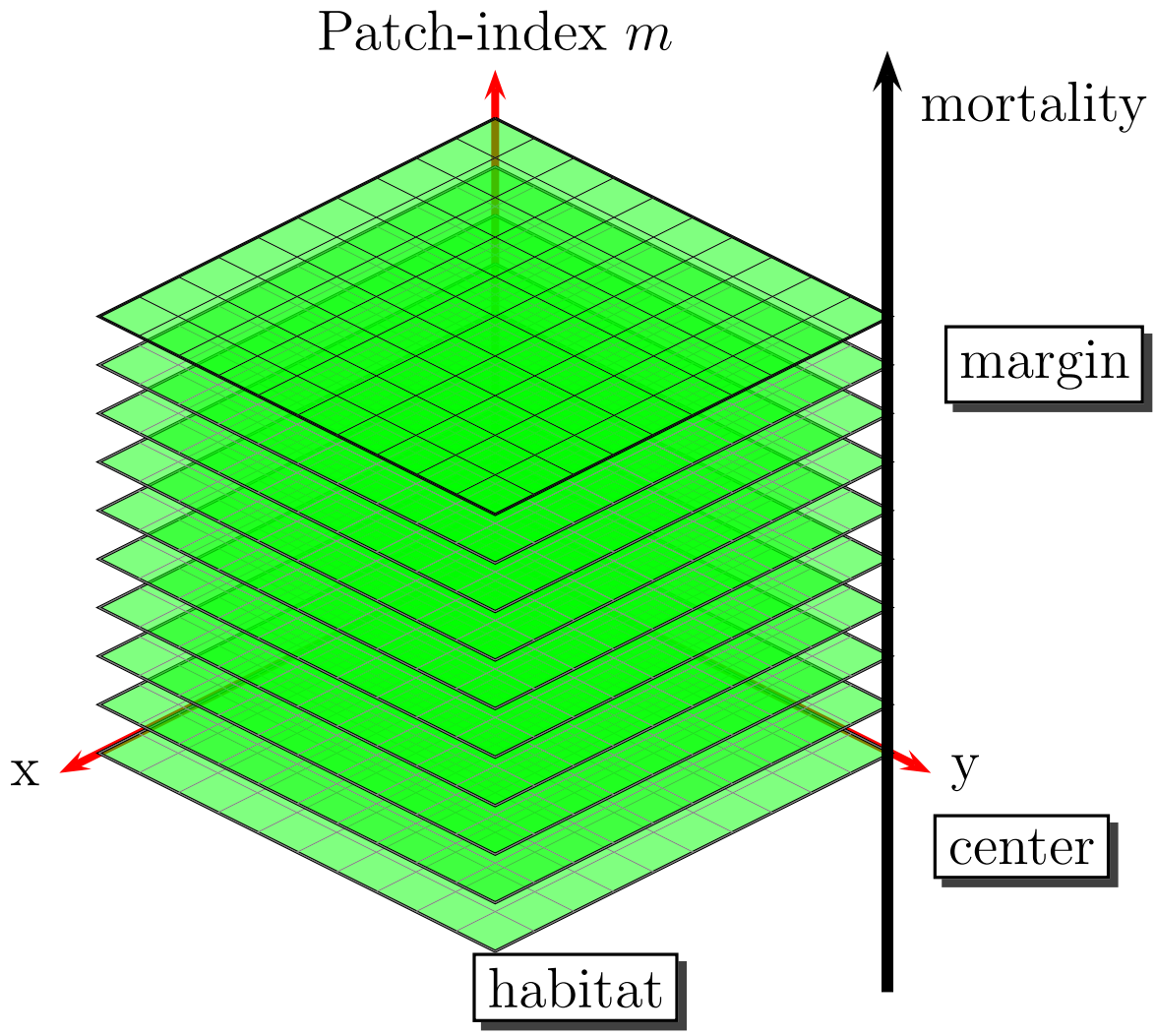



**Figure 2.1.:** The arrangement of patches and niches in the model. In each patch different resources are arranged in a two-dimensional array of niches. The patches at bottom represent the center of species' range, i.e. the favorable habitats. The patches at the top represent the margin of species' range, i.e. the harsh habitats. The bottom-up arrangement of the patches is supposed to mimic the transition for instance from low to high geographic latitude, while the mortality increases with patch index $m$.

Twenty resource patches are arranged along a one-dimensional chain, as illustrated in Fig. 2.1. This chain of patches represents a one-dimensional cut through the two-dimensional range of a

species. The cut starts at the center and continues to the boundary of this range. At the center, the environment is favourable for the consumer, and becomes harsher towards the boundary. A gradient of up to four patch features (specified below) reflects this change in habitat properties from the center to the boundary. In each patch, resources are arranged in a two-dimensional array with $L \times L$ 'niches', which are labelled with 'trait values' $(j_x, j_y, j_z)$, with $(j_x, j_y) \in [1, L]^2$ being the (integer) coordinates of the niche, and $j_z \in [1, 20]$ being the index of the patch $m$, increasing from the center ($m = 1$) to the boundary ($m = 20$) of the species' range. We assume that a property of each resource changes as one moves from the center to the boundary of a species' range, which is represented by $j_z$ in our model. For example, as climate becomes dryer and/or cooler, the leaves of plants - the food of herbivores - become harder. Consumers are characterized by their mode of reproduction and by their genotype, which for simplicity is denoted by the same trait values (niche coordinates and patch index) as the niches. The consumer genotype has therefore three coordinates (or dimensions) and they are identical with the three coordinates of the niche the consumer is best adapted to.

The model is initiated with a maximum resource biomass $R_j = R_{\max} = 100$ in each niche, and with some niches being occupied by sexual or asexual individuals with a matching genotype. The life cycle of the consumers is tailored to that of species with intermittent mixis such as *Daphnia* (Bell, 1982; Hebert *et al.*, 1988). We take the body mass of an individual as the unit for biomass. Thus, the biomass $P_i$ of consumer $i$ increases from the initial value $P_i = 1$ by asexual reproduction during the growing season according to the equation

$$\dot{P}_i = \lambda \sum_{j_y=1}^{L} \sum_{j_x=1}^{L} \alpha_{ij} P_i R_j - d P_i \,, \tag{2.1}$$

while the resource biomass decreases according to

$$\dot{R}_j = - \sum_{i} \alpha_{ij} P_i R_j \,, \tag{2.2}$$

where the sum is taken over all consumers in the same patch. We assume that stochastic effects are not important during the growing season, because the individuals multiply fast (Hebert *et al.*, 1988). The parameters are the ecological efficiency[iv] $\lambda = 0.2$ (Stephens and Krebs, 1986) and the coupling strength between consumer $i$ and resource $j$, $\alpha_{ij} = 1/e^S$, where $S$ is the squared distance between genotypes $i$ and $j$, i.e., the coupling declines exponentially with the squared distance. When the distance in any of the three directions is larger than 2, or when a resource $j$ is not present in a patch, we set $\alpha_{ij}$ to zero. A consumer can only efficiently feed on those resources that are sufficiently close to its own genotype in resource space, i.e., when $S$ is small. The death rate $d$ and the resource array size $L$ can vary between patches. Variation in

[iv] The efficiency at which energy is transferred from one trophic level to another is called **ecological efficiency**. **Trophic level**: step in a nutritive series, or food chain, of an ecosystem. The organisms of a chain are classified into these levels on the basis of their feeding behaviour. The first and lowest level contains the producers, green plants. The plants or their products are consumed by the second-level organisms - the herbivores, or plant eaters. At the third level, primary carnivores, or meat eaters, eat the herbivores; and at the fourth level, secondary carnivores eat the primary carnivores. - http://www.britannica.com

$L$ is implemented such that from patch $m$ to patch $m+1$, resources in the last row and the last column in resource space are deleted.

Each consumer continuously feeds on its resources until the growth rate of the biomass $\dot{P}_i$ falls to zero according to Eq. 2.1. If a consumer continues to eat beyond this moment in time, it would obtain less energy from the resources than what it needs for metabolism. Consumers that cannot multiply any more lay eggs and die.

The starting configuration for the next season is then calculated: resources regrow partially according to the equation

$$\Delta R_j = G(1 - R_j/R_{\max}) = \frac{G}{R_{\max}} \underbrace{\left(R_{\max} - R_j\right)}_{R_j^{\text{consumed}}} . \tag{2.3}$$

With our choice of $R_{\max} = 100$, $G$ represents the regrowth percentage of resources. Eq. (2.3) implies that $G$ percent of the exploited resources, $R_j^{\text{consumed}}$, are recovered between the growing seasons. The number of consumer individuals in each patch at the beginning of a new season is chosen from a Poisson distribution with a mean value $n = 20$, which reflects the situation that only few of the many eggs laid at the end of the previous season give rise to surviving individuals at the beginning of the next season. Due to the twofold cost of sexual reproduction (Maynard Smith, 1971a), asexuals lay twice as much eggs as sexuals having the same biomass. Therefore, each initial individual is sexual with probability

$$p_{\text{s}} = \frac{\sum_{i\,\text{sex.}} P_i}{\sum_{i\,\text{sex.}} P_i + 2\sum_{i\,\text{parthenog.}} P_i} , \tag{2.4}$$

and parthenogenetic with probability $1 - p_{\text{s}}$, with the $P_i$ being the biomasses at the end of the previous season. The regrowth percentage of resources $G$ and the average number of initial individuals per patch $n$ can also vary between patches.

The genotype of a parthenogenetic individual is randomly chosen among the genotypes of parthenogens present in the previous season, with weights proportional to their final biomass. The genotype of a sexual individual is determined by randomly choosing two parent genotypes with probabilities proportional to their biomass at the end of the previous season, and by assigning to the offspring a genotype chosen from a Gaussian distribution around the mid-parent value in each of the two or three dimensions of genotype space, rounded to the nearest integer that still lies within the allowed range $[1, L]$. Unless indicated otherwise, the variance of the Gaussian distribution is $V_{\text{g}} = 2.5^2$ in the $x-$ and $y-$ direction (i.e., the within-patch genetic variance), and $V_{\text{g}z} = 1$ in the $z-$ direction (the between-patch genetic variance). This means that the offspring of sexuals can obtain a genotype that makes it better adapted to a neighbouring patch than to the patch in which it resides. This rule implements the fact that sexual reproduction can destroy adaptation as well as generate it. When the $z$ component of the genotype $i$ of an offspring differs from the patch in which it resides, it feeds less efficiently on the resources, since $\alpha_{ij}$ is smaller than 1 for all resources $j$ in that patch.

Finally, with a small probability $u = 0.001$, the offspring of sexual individuals becomes parthenogenetic, implementing the 'frozen niche variation hypothesis' of Vrijenhoek (1979),

which is based on the fact that parthenogenetic lineages can arise in sexual populations. This implementation is aimed to examine the resistance of sexual populations to invasions of asexual clones.

**Table 2.2.:** List of Parameters applied in the model

| Symbol | Meaning |
|---|---|
| $P_i$ | biomass of consumer $i$ |
| $R_j$ | resource biomass in niche $j$ |
| $R_{\max}$ | maximum resource biomass in a niche |
| $\alpha_{ij}$ | coupling strength between consumer $i$ and resource $j$ (resource in niche $j$) |
| $\lambda$ | ecological efficiency |
| $d$ | death rate |
| $L$ | resource diversity measured by the resource array size in each of the two dimension in a patch |
| $G$ | regrowth percentage of resources, i.e., ratio of resource biomass growth between two subsequent seasons to exploited resource biomass. |
| $n$ | average number of initial individuals of every consumption season per patch |
| $\eta$ | migration rate of offspring to a neighboring patch |
| $V_{\mathrm{g}}$ | within-patch genetic variance of sexual offspring: genotypes of offspring are chosen from a Gaussian distribution around the mid-parent value in each of the two dimensions of genotype space within a patch and then rounded to the nearest integer that still lies within the allowed range $[1, L]$. |
| $V_{\mathrm{gz}}$ | between-patch genetic variance of sexual offspring: genotypes of offspring are chosen from a Gaussian distribution around the mid-parent value in the third dimension of genotype space alongside the one dimensional chain of the 20 patches and then rounded to the nearest integer that still lies within the allowed range from 1 to 20. |
| $u$ | sexual-to-asexual mutation rate: each sexual offspring can mutate to an asexual offspring, based on the fact that parthenogenetic lineages can arise in sexual populations. (Vrijenhoek, 1979) |

Before the onset of resource consumption, each individual is allowed to migrate to each neighbouring patch with a migration probability $\eta$ (e.g., $\eta = 0.01$ means that to each neighbouring patch 1% of the local individuals may migrate). While there is only one neighbouring patch to the first and last patch, all other patches have two neighbours. Then, we apply again equations (2.1) and (2.2), starting with an initial consumer biomass in each niche $i$ that is equal to the number of individuals in this niche.

The parameters applied in the model are outlined in Table 2.2. The iteration of the computer simulation is illustrated by Fig. 2.2. We iterated this process for 1000 seasons before evaluating the resulting geographic distribution of sexual and asexual reproduction, the genetic variance of the sexual population, and the temporal change in resource use.

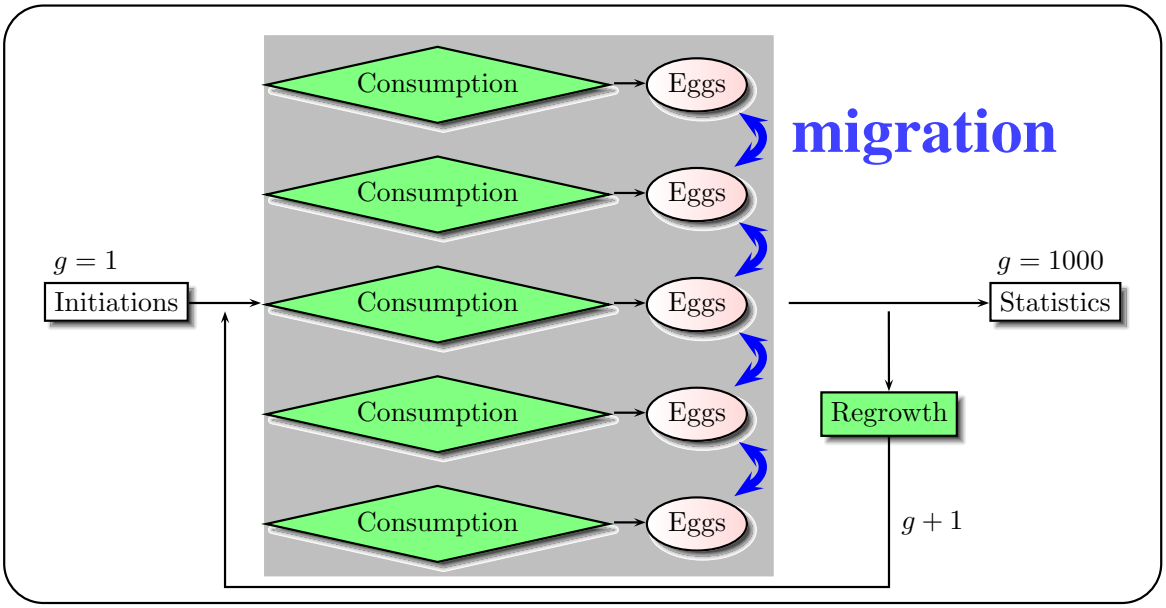



**Figure 2.2.:** The simulation iterates the life cycle of species with intermittent mixes such as *Daphnia*. The first iteration begins with a maximum resource biomass $R_{\max} = 100$ for each resource, and with $n$ consumer individuals of randomly chosen mode of reproduction and genotypes in each patch. Each iteration consists of population dynamics driven by resource consumption, reproduction via random mating followed by selection of eggs to survive until next season/iteration, and migration of eggs to neighboring patches. Between two subsequent seasons, $g$ and $g + 1$, resources partially regrow. After 1000 seasons/iterations, when the equilibrium distribution of sexual reproduction has been reached, the proportion of sexual individuals in each patch is evaluated.

## 2.3 Results

### 2.3.1 A gradient of ecological parameters results in geographic distribution of sexual reproduction

#### Advantage of sexual reproduction varies with each single ecological parameter

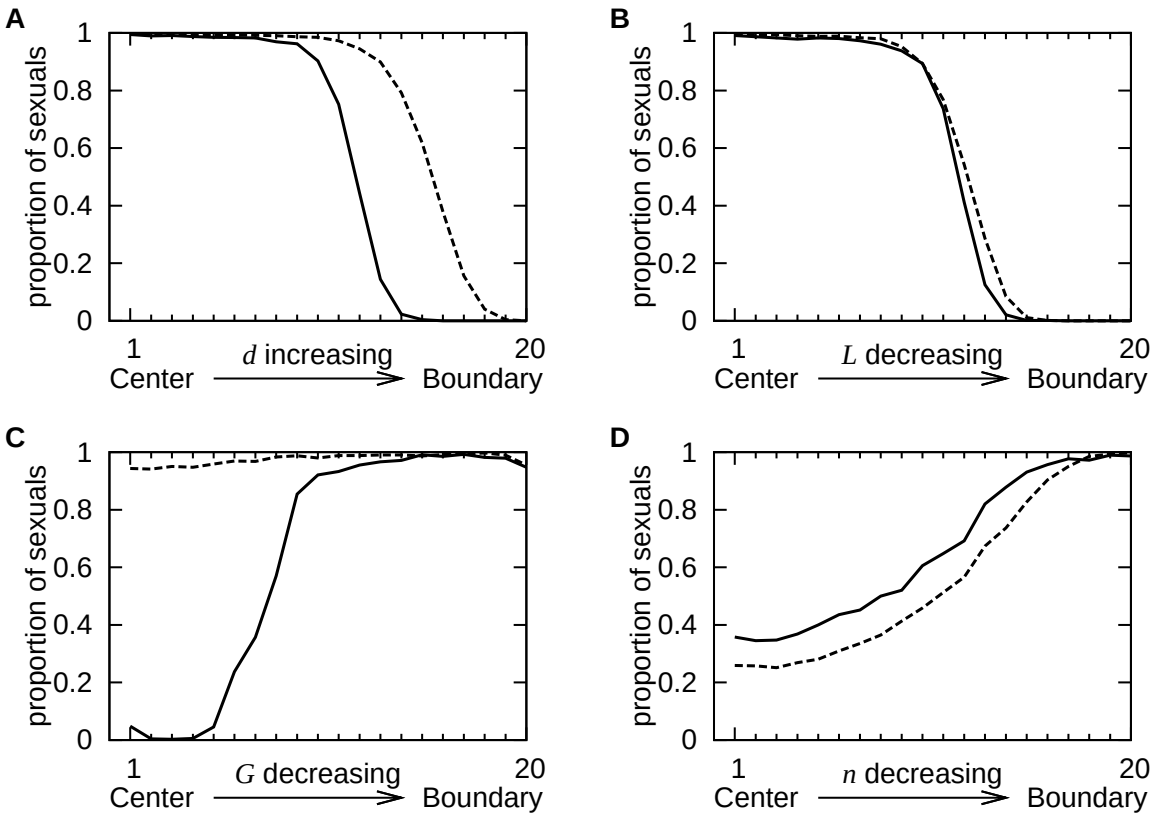



**Figure 2.3.:** Average equilibrium proportion of sexuals in the 20 patches, with the index increasing from the center (1) to the boundary (20). The parameters that vary between patches are (A) the death rate $d$ increasing in constant steps from 25 (in patch 1) to 53.5 (in patch 20), (B) the resource array size $L$ decreasing in constant steps from 20 (in patch 1) to 1 (in patch 20), (C) the regrowth percentage of resources $G$ decreasing in constant steps from 100 (in patch 1) to 5 (in patch 20), and (D) the average number of initial individuals per patch $n$ decreasing in constant steps from 200 (in patch 1) to 10 (in patch 20). The parameters that are not varied between patches are $d = 30$, $L = 20$, $G = 20$ (i.e., 20% of the exploited resource biomass is recovered between the seasons) and $n = 20$. The remaining parameters are: sexual-to-asexual mutation rate $u = 0.001$; migration rate $\eta = 0.01$; within-patch genetic variance of sexual offspring $V_g = 2.5^2$, between-patch genetic variance $V_{gz} = 1$. For comparison, the dashed lines show the curves obtained when the resources are identical in all patches (in which case we set $V_{gz} = 0$ and $j_z$ identical in all patches). The curves in A and B are results averaged over 1000 runs of the simulation, while the curves in C and D are results averaged over 100 runs.

Fig. 2.3 shows the average proportion of sexuals in each patch obtained after a sufficiently long time, when an equilibrium has been reached, averaged over 100 or 1000 runs of the simulation (as a compromise between good statistics and computational time costs). In Fig. 2.3A, the death rate $d$ is increased with increasing patch index, varying overall by a factor of 2. In Fig. 2.3B, the number of different resources, $L^2$, is decreased from $20^2$ to 1 with increasing patch index. In each case, the proportion of sexuals decreases from (almost) 100% to (almost) 0% with increasing patch index (i.e. with increasing harshness of the environment). These results are still independent of the initial distribution of genotypes and modes of reproduction. Compared with the simpler situation with an identical set of resources in all patches (dashed lines), the percentage of sexuals decreases faster in the model with different sets of resources (solid lines). This is based on the fact that sexual offspring may be better adapted to a neighbouring patch according to the third trait value of their genotype, while asexual offspring retain the (well-adapted) genotype of the parent. The contrast reflects the disadvantage of sexual reproduction destroying well-adapted genotypes via gene recombination. In Fig. 2.3C, the regrowth percentage of resources $G$ is decreased with increasing patch index. In Fig. 2.3D, the average number of initial individuals per patch $n$ is decreased with increasing patch index. In contrast, the proportion of sexuals increases with increasing patch index in these cases. In patches with extremely large values of $G$ and $n$, the assumptions of the original structured resource model with short supply (Scheu and Drossel, 2007) are violated. Therefore, failing to explain the maintenance of sex is not surprising. In Fig. 2.3C, the comparison with the simpler situation, where all patches contain an identical set of resources (dashed line), is the most significant. In the model version chosen for the present study (solid line), the proportion of sexuals increases from (almost) 0% to (almost) 100%, while the proportion of sexuals is over 90% in all patches in the simpler situation. This again is due to the possibility of sexual offspring being adapted to a neighbouring patch and therefore not capable to efficiently feed on the resources in its own patch. In case of large $n$ (Fig. 2.3D), however, the proportion of sexuals is larger when $j_z$ and $V_{gz}$ are involved (solid line) than when all patches contain an identical set of resources (dashed line). When $n$ is large, there is a considerable number of migrants that reside in a neighboring patch than that of their parents. While the sexual offspring might be adapted to the neighboring patch due to genetic variation in the $z$ direction, the asexual migrants are for sure not adapted, thus the asexuals are to a great extent prevented from gaining new niches via migration.

## Geographic parthenogenesis emerges with gradient of two ecological parameters

In nature, a gradient of two or more ecological parameters is common. When a reasonable decrease in $G$ or $n$ is superimposed to the increase in $d$ or the decrease in $L$ (Fig. 2.4), the pattern of geographic parthenogenesis emerges, i.e., sexual reproduction dominates in the center (patch 1), while asexual reproduction dominates at the boundaries of species' range (patch 20). The simultaneous gradient of $d$ and $L$ results in the pattern of geographic parthenogenesis. The comparison between the simpler situation (identical set of resources in all patches) and the situation with an additional dimension (different set of resources) represents the consequence of local adaptation. With small $n$, sexual offspring suffer a disadvantage, since some of them have a trait value in $z$ direction differing from the patch index, i.e. the trait value in $z$ direction of resources in that patch. With large $n$, i.e., large amount of migrants, sexual offspring are

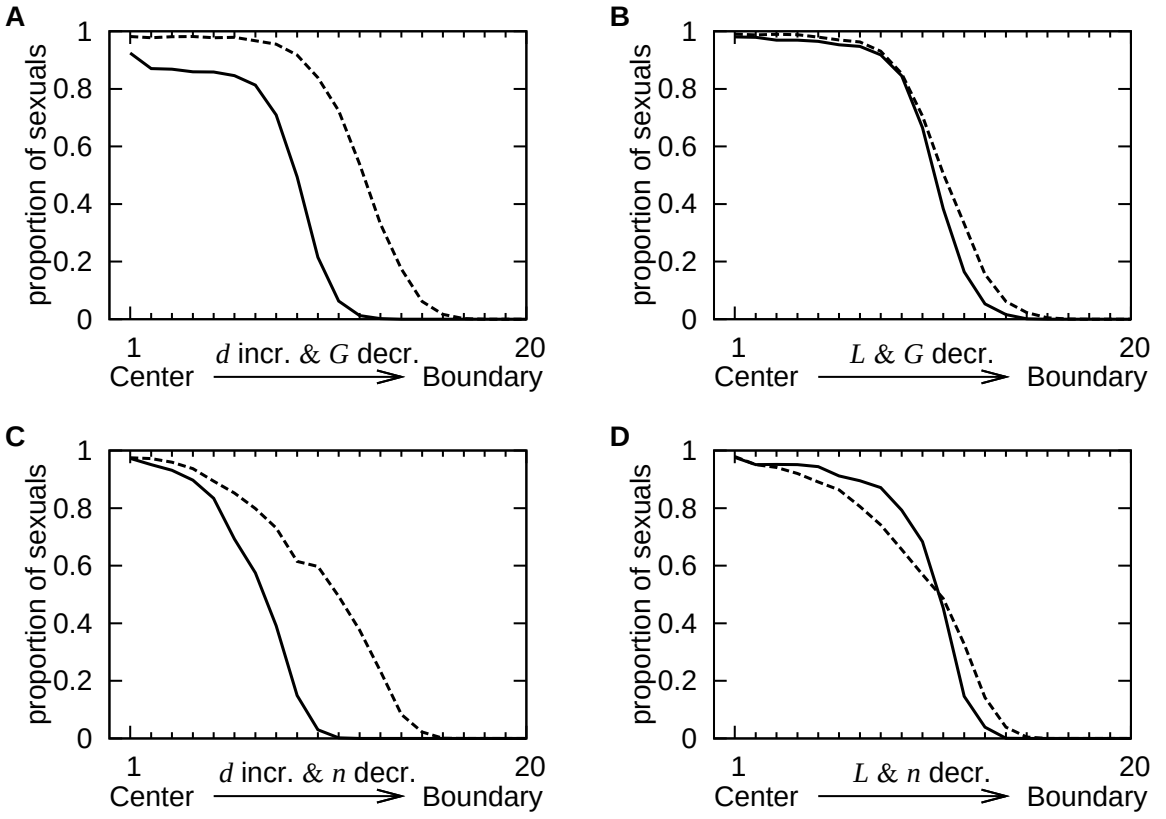



**Figure 2.4.:** Average equilibrium proportion of sexuals in the 20 patches, with the index increasing from the center (1) to the boundary (20). The parameters that vary between patches are (A) the death rate $d$ increasing in constant steps from 25 to 53.5 and the regrowth percentage of resources $G$ decreasing in constant steps from 40 to 2, (B) the resource array size $L$ decreasing in constant steps from 20 to 1 and $G$ decreasing in constant steps from 20 to 1, (C) $d$ increasing in constant steps from 30 to 58.5 and the average number of initial individuals per patch $n$ decreasing in constant steps from 50 to 12, (D) $L$ and $n$ decreasing as in B and C, respectively. The parameters that are not varied between patches are $d = 30$ (expect for graph B, where $d = 25$), $L = 20$, $G = 20$ (i.e., 20% of the exploited resource biomass is recovered between the seasons) and $n = 20$. The remaining parameters are: sexual-to-asexual mutation rate $u = 0.001$; migration rate $\eta = 0.01$; within-patch genetic variance of sexual offspring $V_g = 1.5^2$ in graphs A and B, while $V_g = 2.5^2$ in graphs C and D; between-patch genetic variance $V_{gz} = 1$. For comparison, the dashed lines show the curves obtained when the resources are identical in all patches (in which case we set $V_{gz} = 0$ and $j_z$ identical in all patches). The curves in A and B are results averaged over 1000 runs of the simulation, while the curves in C and D are results averaged over 100 runs.

advantaged, since some of the sexual migrants are adapted to local resources and can therefore efficiently exploit the resources.

### 2.3.2 Influence of migration

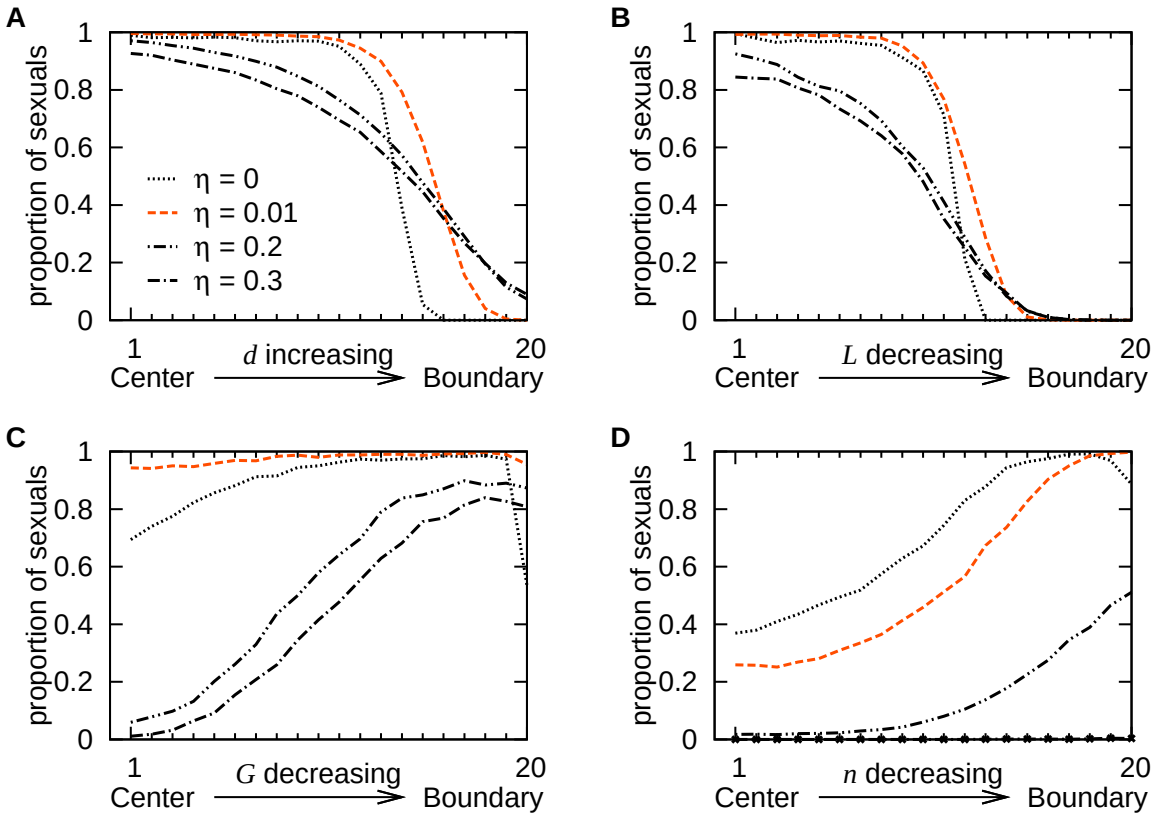



**Figure 2.5.:** Influence of the migration rate $\eta$ on the equilibrium proportion of sexuals in the 20 patches from the center (1) to the boundary (20). These results are from the model with an identical set of resources in all patches, i.e., without the third trait value. In the graphs, the red dashed curve is the same as the dashed curve in Fig. 2.3, since all parameters are identical. The curves in A are results averaged over 1000 runs of the simulation, so are the red dashed curve in B and the $\eta = 0$ curve in C, while all the other curves are results averaged over 100 runs.

Fig. 2.5 shows the influence of the migration rate $\eta$ in the simpler situation with patches containing an identical set of resources. The advantage of sexuals increases at first with increasing migration rate, because sexual migrants can counteract the local loss of genetic variance. The advantage of sexuals is larger when the genetic variance is larger, because sexual offspring can more easily exploit niches that have not been depleted in previous seasons, and the competition between sexual siblings (and the resource conflict with parent generation) can thus be more efficiently reduced. When the migration rate becomes even larger, the curve becomes more flat. With high migration rate, asexual offspring gain new niches in neighboring patches, which reduces the advantage of sexual offspring to some extent. In Fig. 2.5A, B, and C, the source-sink effect prevents the proportion of sexuals from becoming constant; while in Fig. 2.5D, the pro-

portion of sexuals vanishes in all patches with excessively high migration rate. High migration rate combined with large average initial number of individuals per patch makes a large number of migrants, i.e., the number of asexual migrants is large. Effectively, asexual populations gain much more available resources via excessive migration, and thereby drive sexual populations to extinction.

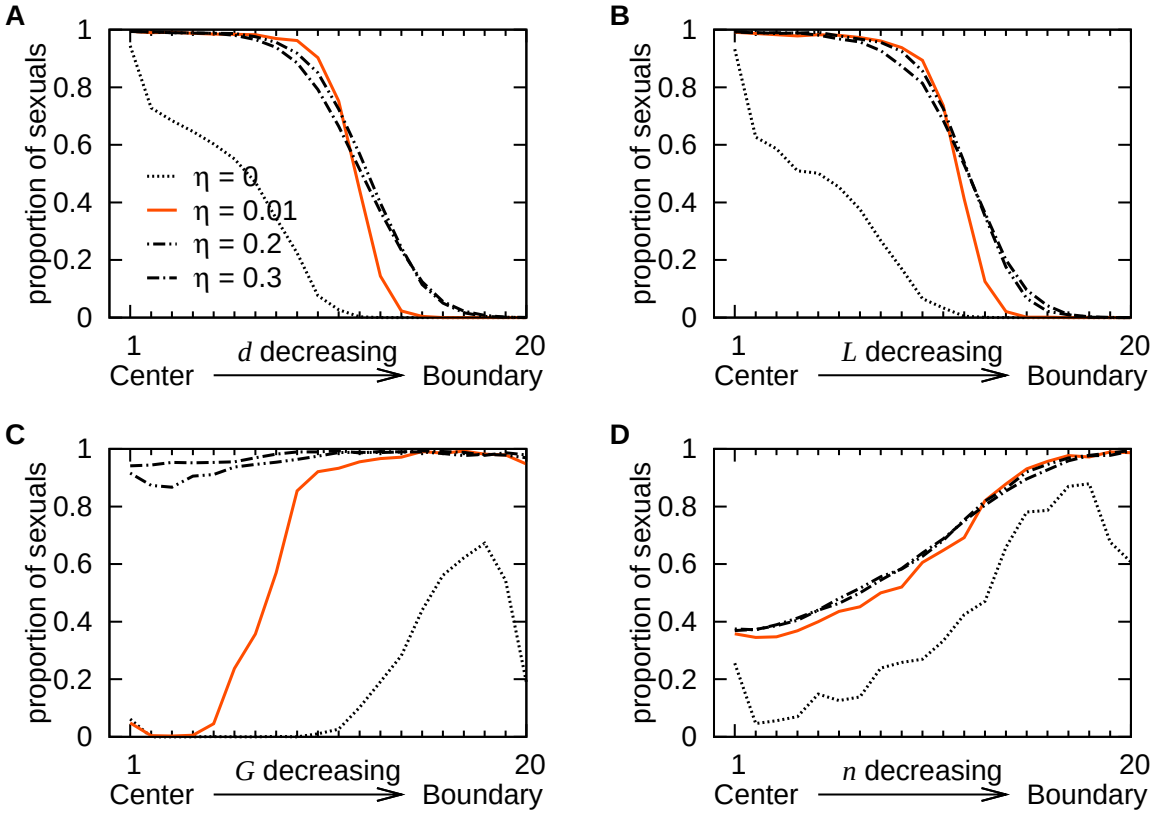



**Figure 2.6.:** Influence of the migration rate $\eta$ on the equilibrium proportion of sexuals in the 20 patches from the center (1) to the boundary (20). These results are from the model with a different set of resources denoted with the third trait value $j_z$ in each patch.In the graphs, the red solid curve is the same as the solid curve in Fig. 2.3, since all parameters are identical. The curves in A are results averaged over 1000 runs of the simulation, so are the red dashed curve in B, and the $\eta = 0$ curve in B and C, while all the other curves are results averaged over 100 runs.

Fig. 2.6 shows the influence of the migration rate $\eta$ in the chosen version of our model with patches containing different set of resources, denoted by $j_z$. The advantage of sexuals again increases at first with increasing migration rate, because sexual migrants can here again counteract the local loss of genetic variance. The advantage of sexuals is larger when the genetic variance is larger, for the same reason mentioned above for the simpler version, i.e., sexual offspring encounter a reduced competition for resources. Specially, in this version some sexual migrating offspring can be adapted to the new patch, while asexual clones are never adapted to neighbouring patches, since their trait values are identical to their local parents' in all three dimensions. We also investigated the case where migration happens before selecting offspring for the next season (which can be interpreted as egg dispersal); here we found no significant changes in the behavior of the curve. When the migration rate becomes even larger, the curve becomes

more flat. In Fig. 2.6A, B, and D, the source-sink effect (Dias, 1996) prevents the proportion of sexuals from becoming constant; while in Fig. 2.6C, the proportion of sexuals is over 90% in all patches with large migration rate. Even if the regrowth percentage of resources is 100%, the reduced sibling competition and a considerable possibility of local adaptation among sexual migrants bring a great advantage for sexual populations. The asexual migrants, in contrast, are by no means adapted to the neighboring patch they migrate to, besides the intense competition between clones of the same mother fully eliminates the two-fold number of offspring.

### 2.3.3 Influence of genetic variance of sexual offspring

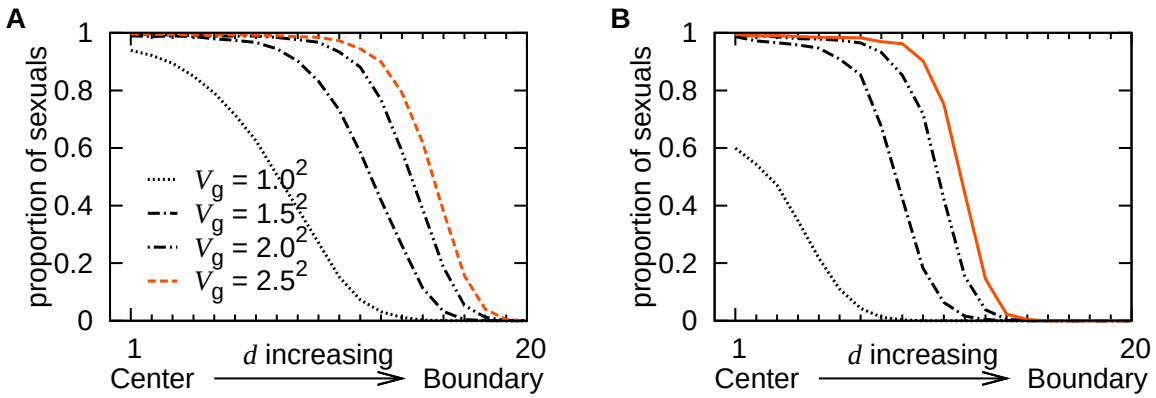



**Figure 2.7.:** Influence of the within-patch genetic variance of sexual offspring $V_g = \sigma^2$ on the equilibrium proportion of sexuals in the 20 patches from the center (1) to the boundary (20). In both graphs, the red (dashed or solid) curve is the same as that in Fig. 2.3(a)A, since all parameters are identical. The curves in A show the patterns obtained when the resources are identical in all patches (in which case we set $V_{gz} = 0$ and $j_z$ identical in all patches). The curves in both graphs are results averaged over 1000 runs of the simulation.

Fig. 2.7 shows the influence of the within-patch genetic variance of sexual offspring in the simpler situation with an identical set of resources in all patches (Fig. 2.7A) and in the chosen version of our model with a different set of resources denoted by $j_z = m$ for the patch $m$ (Fig. 2.7B). The advantage of sexuals increases with increasing $V_g$ in both cases, because the advantage of sexuals is larger when the genetic variance is larger, because sexual offspring can more easily exploit niches that have not been depleted in previous seasons by their parents, and the competition between sexual siblings (and the resource conflict with parent generation) can thus be more efficiently reduced. The dynamics of resource usage and the genetic variance of sexual population will be investigated in the next section.

Fig. 2.8 shows the influence of the between-patch genetic variance of sexual offspring in the chosen version of our model. The advantage of sexuals decreases with increasing $V_{gz}$. This investigation clearly represents the disadvantage of sexual reproduction destroying local adaptation. With a 1% migration rate, most of the offspring reside in the same patch as their parents. It is therefore disadvantageous for the sexuals to have part of their offspring adapted to a neighboring patch rather than their own and not able to efficiently exploit resources in the patch. This makes it easier for the asexual population to win the patch with their high reproductivity.

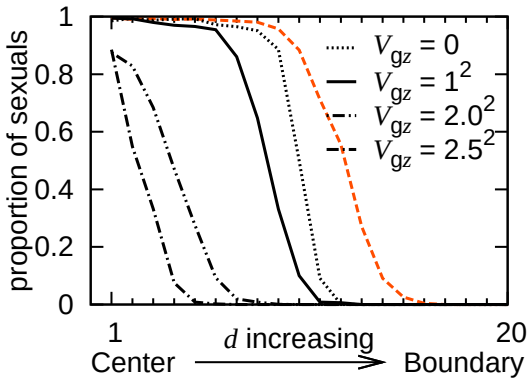



**Figure 2.8.:** Influence of the between-patch genetic variance of sexual offspring $V_{gz} = \sigma_z^2$ on the equilibrium proportion of sexuals in the 20 patches from the center (1) to the boundary (20). The parameter that vary between patches is the death rate $d$ increasing in constant steps from 30 (in patch 1) to 58.5 (in patch 20). The parameters that are not varied between patches are $L = 20$, $G = 20$ (i.e., 20% of the exploited resource biomass is recovered between the seasons) and $n = 20$. The remaining parameters are: sexual-to-asexual mutation rate $u = 0.001$; migration rate $\eta = 0.01$; within-patch genetic variance of sexual offspring $V_g = 2.5^2$. For further comparison, the red dashed lines show the curves obtained when the resources are identical in all patches (in which case we set $V_{gz} = 0$ and $j_z$ identical in all patches). The curves are results averaged over 100 runs of the simulation.

Ignoring this consideration by excluding the $z$ component, as in the simpler situation (the red dashed line in Fig. 2.8), the proportion of sexuals becomes larger, even larger than in the chosen version with $V_{gz} = 0$. As discussed previously, sexual migrants can counteract the local loss of genetic variance. If the patch, however, has a different set of resources than the "native" patch of the migrants, they cannot efficiently exploit the local resources. Those sexual migrants are less likely to contribute to the local gene pool and prevent the local loss of genetic variance. Nevertheless, even with the disadvantage of sexual reproduction breaking up local adaptation, there is still a wide range of ecological parameters, where sexual reproduction prevails with its advantage of generating new adaptations, which makes more niches available for sexual populations.

### 2.3.4 Temporal patterns of resource usage and genetic variance of sexual population

Having established the winning mode of reproduction under a variety of conditions, we then evaluate the genetic variance of the sexual population in each patch, and the rate at which the barycenter of sexual population[v] moves within the patch. Fig. 2.9A and B show the genetic variance of the sexual population for the first 16 patches (where the sexuals are present most of the time). For different values of $\eta$, Fig. 2.9A shows that migration enhances the genetic variance of sexual population, since sexual migrants can counteract the local loss of genetic variance. For different values of $V_g$, Fig. 2.9B shows the genetic variance of sexual population increases with increasing genetic variance of sexual offspring. The variance of the population is larger

[v] **Barycenter of sexual population** is determined by the average coordinates of all sexual individuals in the patch.

than twice $V_g$, which is the value expected for a population with random mating and without selection. The selective advantage of exploiting unused resources thus manifests itself in the increased genetic variance of the population. The variance of the population decreases towards the value $2V_g$ only in the last patches, where the advantage of exploiting unused resources is small. In all patches, the sexual population covers only part of the niches.

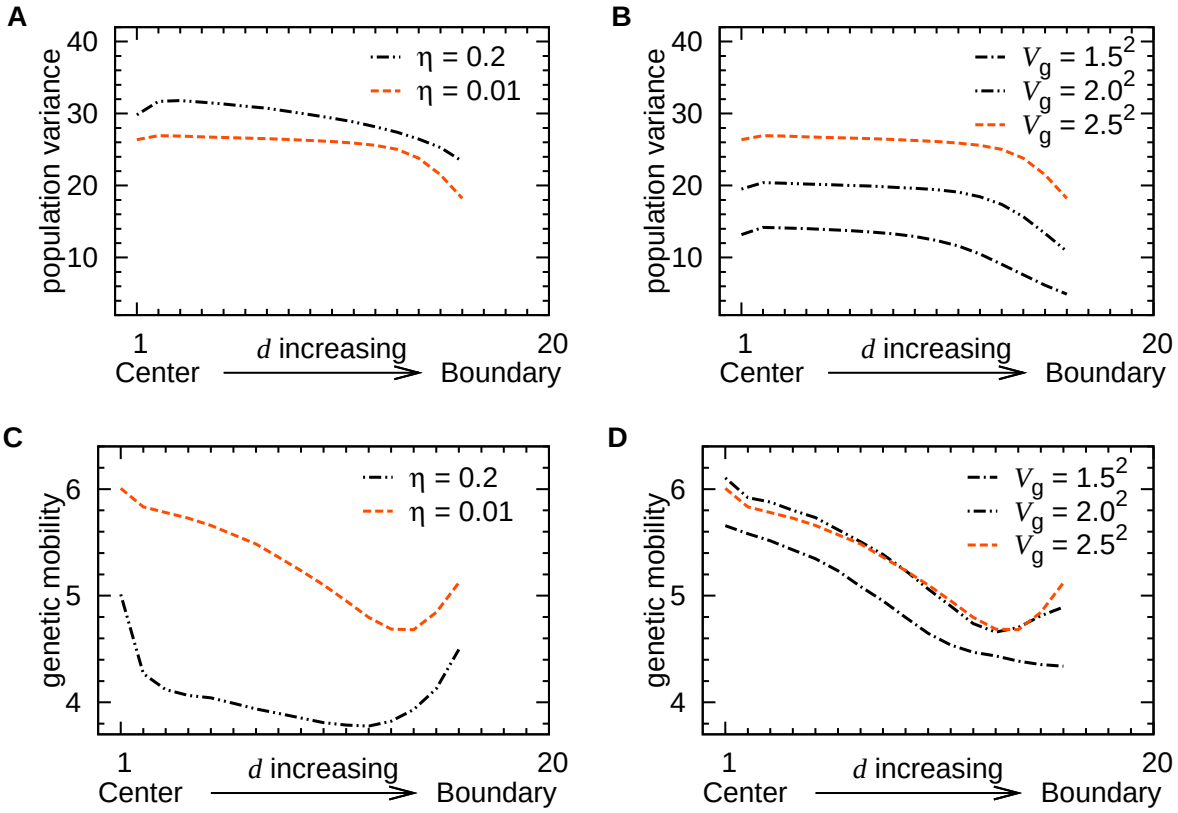



**Figure 2.9.:** Genetic variance of the sexual population (A and B) and the average distance over which the barycenter of the sexual population moves during five seasons (C and D), in the first 16 patches (where the sexuals exist most of the time). The results are obtained when the resources are identical in all patches. In all graphs, the red dashed curve is produced with the same parameters as the dashed curve in Fig. 2.3A, while the other curves are produced with different values of the migration rate $\eta$ (A and C) and with different values of the within-patch genetic variance of sexual offspring, $V_g = \sigma^2$ (B and D).

Fig. 2.9C and D show the average distance over which the barycenter of the sexual population moves in five seasons. It might look surprising that this distance decreases with increasing migration rate (Fig. 2.9C), but we will show later in this section that it is actually expected. The distance over which the barycenter of the sexual population moves is greatest where selection pressure is largest, and it is less when $V_g$ is smaller. This means that the selection pressure towards using unexploited resources causes the sexual population to change continuously. The increase in genetic mobility with a smaller $V_g = 2^2$ (Fig. 2.9D) in favorable patches is caused by the constraint of resource space. As shown in Fig. 2.9B, the population variance is considerably high with $V_g = 2.5^2$. Therefore, the barycenter moves only in a small area near the center of the patch. A smaller $V_g$, $2^2$ in this case, reduces the confinement of the barycenter and slightly advances its mobility. Besides, the increase of part of the curves in the last two patches is due to

the sexuals vanishing from the patch and immigrating anew. Fig. 2.10 shows this motion of the sexual population for one simulation run, for three neighbouring patches, and for both the *x*- and the *y*-coordinate of the barycenter in genotype space. The population moves back and forth in both coordinates and thus visits all niches over a greater period of time. Due to migration the motion in neighbouring patches is partially coupled, which is evaluated in the next paragraph.

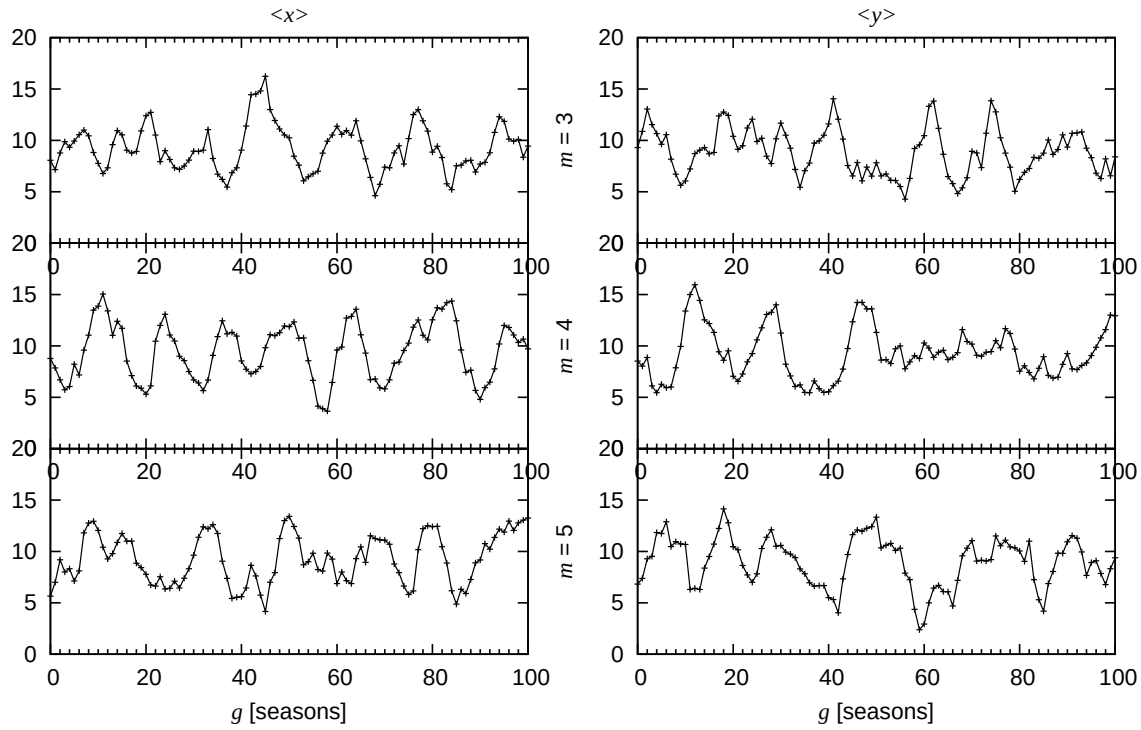



**Figure 2.10.:** Motion of the barycenter of the sexual population, represented by the two coordinates $\langle x \rangle$ and $\langle y \rangle$, in the third, fourth and fifth patch for a time window of 100 seasons at equilibrium. The curves are produced with the same parameters as the dashed curve in Fig. 2.3A.

To determine the coupling of the motion of the barycenter of the sexual population in neighbouring patches, we evaluated the correlation[vi] of the barycenters of the sexual population in the *x*-coordinate (Fig. 2.11). Fig. 2.11A shows that the correlation increases with increasing migration rate, which explains the slower movement of the barycenter of the sexual population at higher migration rate (Fig. 2.9C). When the motion of the barycenter is strongly coupled, it is unlikely to have a migrant with a genotype that is far away from the barycenter of the local sexual population. Therefore, the possibility of a migrant driving the barycenter over a large distance is largely reduced. Fig. 2.11B shows the influence of the genetic variance of sexual offspring on the correlation. The correlation decreases with increasing genetic variance, as expected.

[vi] The correlation function is defined by

$$\mathrm{Corr}(x_1, x_2) = \frac{\langle x_1 x_2 \rangle - \langle x_1 \rangle \langle x_2 \rangle}{\sqrt{\mathrm{Var}(x_1)\mathrm{Var}(x_2)}}\,.$$

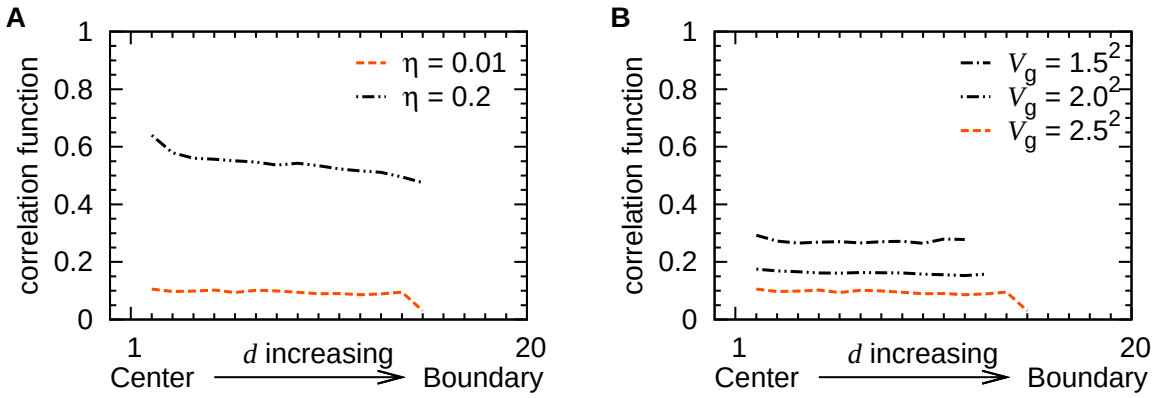



**Figure 2.11.:** Correlation of barycenters of the sexual population between neighboring patches, in one of the two coordinates (here $\langle x \rangle$). The red dashed curve produces with the same parameters as the dashed curve in Fig. 2.3A, while the other curves are produced with different values of the migration rate $\eta$ (A)and with different values of the within-patch genetic variance of sexual offspring, $V_g = \sigma^2$ (B).

## 2.4 Discussion

We have investigated the advantages and disadvantages of sexual reproduction in a model that explicitly takes into account the interaction between resources and consumer individuals. The model is guided by the assumption that resources are the most important factor determining the mode of reproduction (Bell, 1982, 1988; Ghiselin, 1974; Williams, 1975). Building on the previous models of Scheu and Drossel (2007), we explored and discussed the spatial and temporal dynamics in resource use and illustrated the results graphically. By arranging several patches in a chain, mimicking the transition from the center to the boundaries of species' range, our model produced patterns of sexual and parthenogenetic reproduction that resembled that of geographic parthenogenesis, i.e. with sexual lineages dominating in the center and parthenogenetic lineages at the boundary of a species' range (Kearney, 2006; Vandel, 1928). This was achieved by simply varying mortality and resource number along a spatial gradient. The finding that mortality has a strong influence on the reproductive mode is in agreement with the observation that asexual organisms are more frequent in transient, ecotonal, disturbed or marginal environments, like deserts (Kearney, 2003), which are associated with high mortality.

Graphics on the dynamics of resource use illustrated that the genetic variance in sexual populations was strengthened substantially in 'favorable' environments in the framework of this model. The genetic variance of the sexual population and the rate at which resource use changed with generations were largest when the advantage of the sexual reproduction was largest and when the sexual reproduction completely dominated the local population.

One advantage of sexual reproduction is that sexual offspring can exploit resources that have not been used for a long time and therefore abundant. On the other hand, its disadvantage is that adaptation can be destroyed at the same time. This is because the offspring genotype may become that of a recently heavily exploited resource, or one that fits better into a neighbouring patch than into the patch where the individual resides. In addition, there is always the twofold cost of sex (Maynard Smith, 1978), which in our model is incurred once per season. Due to this combination of advantages and disadvantages, it depends on the values of the parameters

whether sexual or asexual reproduction wins. Thus each of the two modes of reproduction can be the equilibrium mode at a different location in space, and since asexual reproduction is favoured under 'harsh' conditions, it tends to prevail at the boundaries of a species' range, which in our model was represented by patches with high mortality or small number of resources.

In contrast to conventional Tangled Bank models (Bell, 1982), a larger population size does not increase the advantage of sexual reproduction in our model. The reason is that $n$ asexual clones together may cover a wider range of resources than $n$ sexual individuals, because random mating keeps the variance of the sexual population within certain limits (cf. Gorelick and Heng, 2010). When $n$ becomes too large, the unused resources are not sufficient for the sexual population to adapt to, and the advantage of sexual reproduction vanishes. The rule that locally only a few genotypes can coexist is thus a vital ingredient of our model. Furthermore, compared with conventional resource use models (Case and Taper, 1986), our model introduces a temporal component: the sexual population wins due to the fact that it can adapt to the continually changing pattern of resource abundance. This finding resembles Red Queen hypothesis, although they are turned upside down. Red Queen models are based on parasite - host interactions (Hamilton, 1980; Hamilton *et al.*, 1990; Jaenike, 1978), whereas the changes of population composition in space and time in our model are due to feedback mechanisms of resource use (i.e., they are based on bottom-up forces). Notably, resources in our model can be of any kind, abiotic (such as nutrients) or biotic (such as living or dead organic matter), and therefore the model is not necessarily based on co-evolutionary arms races as stated by Red Queen hypothesis.

As the structured resource model (Scheu and Drossel, 2007), the current model uses quantitative genetics, i.e., offspring of sexual individuals have a Gaussian distribution around the midparent value in genotype space. This allows the illustration of resource use dynamics. The underlying assumption is that there is enough genetic variance present in the population that adaptation is not limited by genetic constraints. Our local population sizes are small (around 20 individuals per patch at the beginning of a season, with 20 patches in total), but one has to keep in mind that our chain of patches represents a one-dimensional cut through a two-dimensional space that has a large extension and provides in total enough genetic variation to permit the continuous production of new genetic combinations. Besides, a simpler version of the quantitative genetic model that uses a one-dimensional resource space and in which resources do not change along the geographic gradient, also produces the effect of geographic parthenogenesis (I. Ament, unpublished data).

Probably, the type of genetics used is of minor importance as long as the basal ingredients of the model remain the same, i.e. slow regrowth of resources, stochastic effects due to restrictions on the number of locally coexisting genotypes combined with geographical gradients in density independent mortality and/or in resource diversity. Investigations of the structured model with alternative genetic implementations are needed to show that the results of the presented model are robust. The Tangled Bank theory may thereby be proven as general and can be applied to a wide-range of organisms.

# 3 The advantage of sexual reproduction and geographic parthenogenesis with alternative genetic implementations

As in the previous chapter, here the original population dynamics model (Scheu and Drossel, 2007) with structured resources in short supply is extended to a spatial gradient of consumer mortality, resource diversity, regrowth rate of resources and initial population size. However, instead of the implementation of quantitative genetics as in the previous chapter, here genotypes are modeled by means of explicit genetics. Genotype is implemented by a multilocus model with two alleles at each locus, and with free recombination during production of sexual offspring. By mutation asexuals can also gain new niches with a small probability. The model still adopts random mating for sexuals and clonal reproduction for asexuals. Moreover, other essential assumptions of the original model are also retained, i.e., resources are limited and regrow slowly, only a few consumer genotypes can locally coexist, and the twofold cost of sex is incurred once per season. As stated in the previous chapter, the advantage of sexual reproduction is due to the ability of the sexual population to generate offspring that can use resources that have not been exploited for some time. In this chapter, the model is also simulated with two other alternative genetic implementations, and the pattern of geographic parthenogenesis is obtained just as with quantitative and explicit genetics.

## 3.1 Introduction

The importance of ecology for evolution is widely acknowledged, although it is not always explicitly included in mathematical models. That is, theories about the evolution and maintenance of sexual reproduction focus on genetic mechanisms (De Visser and Elena, 2007; Otto, 2009) and on predator-prey (Salathe *et al.*, 2008; Tobler and Schlupp, 2008) or host-pathogen interactions (Hamilton, 1980; Lively and Dybdahl, 2000; Lively, 2009; Van Valen, 1973). However, considering the high costs of sexual reproduction (Maynard Smith, 1978; Williams, 1975), it remains unclear whether these mechanisms are sufficient to explain the maintenance of sexual reproduction (Otto, 2009; S. West *et al.*, 1999). Ecological processes other than predator-prey or host-pathogen interactions, such as the role of resources and their dynamics, are rarely taken into account, despite early and also recent studies stressing their importance (Bell, 1982, 1988; Olofsson and Lundberg, 2007; Williams, 1975).

Bell (1982), on the other hand, elaborated the Tangled Bank hypothesis, and explained the maintenance of genetic diversity and sexual reproduction through resource use scenarios. However, previous resource-based models did not incorporate feedback mechanisms between resource use and the fitness of progeny with the genotypes adapted to use certain fractions of the resources available. This Red-Queen-like mechanism is first integrated by Scheu and Drossel (2007) in the structured resource model.

In this model resources are structured, with one consumer genotype being able to exploit only a fraction of the resources. The dynamics of resource abundance is explicitly taken into account, so that resource use effectively feeds back to the fitness of progeny. Slow regrowth of

resources combined with stochastic effects due to restrictions on the number of locally coexisting genotypes leads to the prevalence of sexual reproduction over a broad parameter range in spite of the costs of producing males. In contrast, it leads to the prevalence of asexual reproduction when mortality is high or when there are no resources that are exploited considerably more than other resources. By introducing a spatial dimension in this model, we even explained geographic parthenogenesis in the previous chapter.

Variations in sexual reproduction in space, termed geographic parthenogenesis, were first documented by Vandel (1928), but resisted a convincing explanation based on evolutionary theory (Gaggiotti, 1994; Kearney, 2006; Peck *et al.*, 1998). In the previous chapter, feedback between resource use and fitness of progeny has been combined with variations in the spatial distribution of resources. Interestingly, by letting sexual and parthenogenetic species compete, the model produced the typical pattern of geographic parthenogenesis with sexual lineages dominating at the center and parthenogenetic lineages at the boundary of the species' range. In this chapter, we show together with three alternative genetic implementations that details in genetic mechanisms are irrelevant in Tangled Bank models.

In the following, a modified model that differs in three aspects from the one shown in the previous chapter is investigated. First, instead of using quantitative genetics, the modified model is genetically explicit and uses several diallelic[i] loci with free recombination. Second, resources are identical in all patches. Third, asexual population can gain new niches by means of mutation at a arbitrary locus or several arbitrary loci in addition to the sexual-to-asexual mutation. The two ways of implementing the genetics represent two limiting cases: In the prior evaluated model, we implement two or three features, and each of which can assume 20 different values. Here, there are more features (6 - 8), each of which can assume only two values. Both types of model give the same general results concerning the conditions under which sexual reproduction prevails, thus indicating that these results are generic and do not depend on the details of the implementation.

Explicit genetics has notable advantages in our model. For instance, it's possible to model the increase of mutation rate that is stimulated by environmental stress in harsh habitat by including a mutation at arbitrary loci. The feature of explicit genetic approach permits to study the effect of recombination on the genetic diversity of the population, which was not possible in the quantitative genetic model. Via comparison with the dynamics of genetic diversity that results from a null model, the impact of structured resources is clarified. Moreover, the general validity of the structured resource model, and thus the Tangled Bank hypothesis, is strengthened via investigating two more alternative genetic approaches.

## 3.2 The Model

The model describes the population dynamics in twenty resource patches that are arranged along a one-dimensional chain. A gradient of up to four patch features (specified below) reflects the change in habitat properties from the center (patch 1) to the boundary (patch 20) of a species' range. Each patch contains up to $L = 256( = 2^8)$ different "resources", which are labelled by binary numbers from 0 to 255, and which are also referred to as "niches" in the following.

[i] **Diallelic** in Glossary.

Consumers are characterized by their mode of reproduction and by their genotype, which for simplicity is denoted by the same numbers as the resources. The genotype of the consumers is represented by a set of eight diallelic loci. When the two alleles at each locus are labelled 0 and 1, the genotype can be represented by a binary number with 8 bits (Fig. 3.1). A consumer is best adapted to the resource the label of which matches its genotype. This method of implementing a genotype and matching it with resources is similar to the one chosen by Gavrilets and Vose (2005). The resources in this model do not necessarily represent different species, but the different possible ways in which consumers can specialize on resources that differ in some respect. The eight degrees of freedom can thus represent different location (humid, less humid, more or less shady), different manifestation (producing certain defenses or not, having a harder surface), or different parts (upper or lower leaves) etc. of the same type of resource. Due to different search patterns, different digestive abilities, different morphological features, etc., different individuals exploit resources in different ways. Indeed, experiments show that genetically diverse populations can better exploit resources than genetically homogeneous populations (Doncaster *et al.*, 2000). Svanbäck and Bolnick (2005) argue that individuals that differ in their ability to find, handle or digest alternative resources may have different diets.

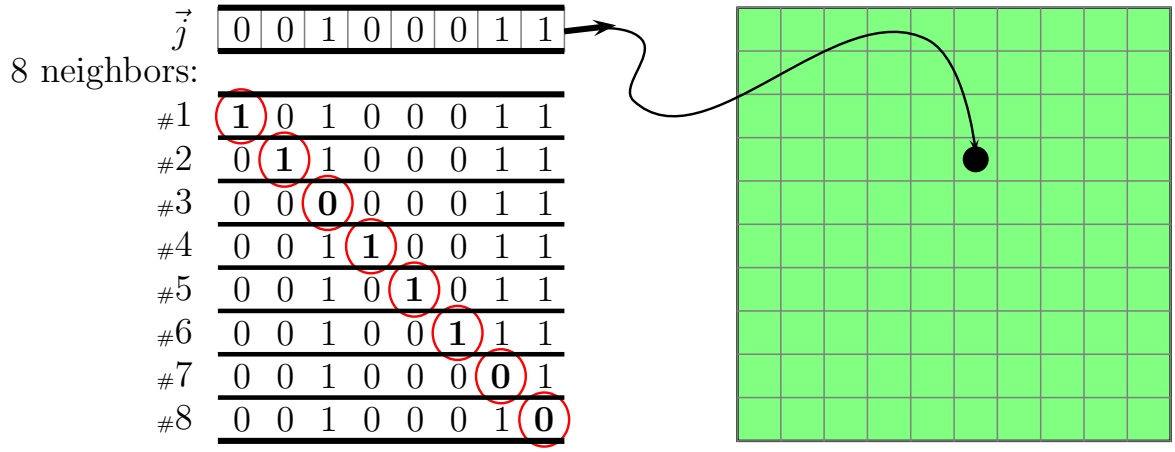



**Figure 3.1.:** Structured resource space with explicit genetics. On the right side: Each patch contains up to $L = 256 = 2^8$ different resources, which are labelled by binary numbers from 0 to 255, and which are also referred to as "niches". On the left side: A consumer genotype is denoted by the same numbers as the resources and is represented by a set of 8 diallelic loci, with the two alleles at each locus labelled 0 and 1. A consumer can exploit the resource the label of which matches its genotype, and resources in "neighboring" niches, the label of which differ only in one bit.

The model is initiated with a maximum resource biomass $R_j = R_{\max} = 100$ for each resource, and with some niches being occupied by sexual or asexual individuals. The life cycle of the consumers is still tailored to that of species with intermittent mixes. Thus, the coupled population dynamics of consumers and resources are described by the same equations as that in the previous chapter (Eq. (2.1) and (2.2)). The ecological efficiency $\lambda$ is chosen to be 0.2 (Stephens and Krebs, 1986) as in the previous chapter. The coupling strength $\alpha_{ij}$ between consumer and resource is set equal to 1 for $i = j$ and equal $e^{-k}$ (with $k$ being 0, 0.5 or 1) when $i$ and $j$ differ in one bit. Otherwise it is set to 0 (Fig. 3.1). In most of the simulations reported below, it is set

$k = 0$, which means that each consumer uses with equal efficiency all nine resources available to it (Fig. 3.1).

In order to mimic increasing harshness of the environment as the patch index increases from center to the boundary of a species' range, the death rate $d$ is increased linearly with increasing patch index, or the number of resources $L$ (or the regrowth percentage of resources $G$, or the average number of initial individuals per patch $n$) is decreased linearly. Variation in the number of resources was implemented such that the resources with the largest labels were removed.

Population dynamics (Eq. (2.1)) is applied for each consumer until its resources becomes depleted, i.e., when the consumer stops feeding and growing. After all consumers have stopped growing, the consumption season is ended. It is assumed that sexual individuals mate at random within the patch, where there is an equal number of males and females, and all females lay the same large number of eggs per biomass. Thus the number of eggs per parent biomass laid by asexuals is twice as large as that of sexuals. The precise number of eggs per female is irrelevant for the following, since the number of eggs that give rise to a surviving individual is small and independent of the total egg number (Cáceres, 1998; García-Roger *et al.*, 2006). Next, the starting configuration for the next season is calculated. Resources regrow partially according to the same equation in the previous chapter (Eq. (2.3)). The number of consumer individuals in each patch at the beginning of a new season is chosen from a Poisson distribution with mean value $n$. The fraction of sexual individuals in the new season is estimated by the Eq. (2.4) in the previous chapter.

The genotype of a parthenogenetic individual is randomly chosen among the genotypes of parthenogens present at the end of the previous season, with weights proportional to their final biomass, and with each bit of the genotype being mutated with a small probability $\mu$. The genotype of a sexual individual is determined by randomly choosing two sexual parent genotypes with probabilities proportional to their biomass at the end of the previous season, and by generating the offspring by free recombination at every locus. Just as for asexual offspring, each bit of the genotype is then mutated with a small probability $\mu$. As in the previous chapter, with a small probability $u = 0.001$, the offspring of sexual individuals becomes parthenogenetic, which is based on the fact that parthenogenetic lineages can arise in sexual populations Vrijenhoek (1979).

Before onset of resource consumption, each individual is allowed to migrate to each neighboring patch with a migration probability $\eta$. Alternatively, we also implemented the case of egg dispersal, where "migration" occurs before selection of the surviving eggs.

We iterated this process for 200 seasons and averaged the resulting final proportion of sexuals in each patch over 1000 runs of the computer simulation.

## 3.3 Results

### 3.3.1 Gradient of ecological parameters results in geographic parthenogenesis

Fig. 3.2 shows the average proportion of sexuals in each of the 20 patches that was obtained after 200 seasons, when an equilibrium had been reached. In the first graph (Fig. 3.2A), the death rate $d$ was increased with increasing patch index, varying in total by a factor of 3.5;

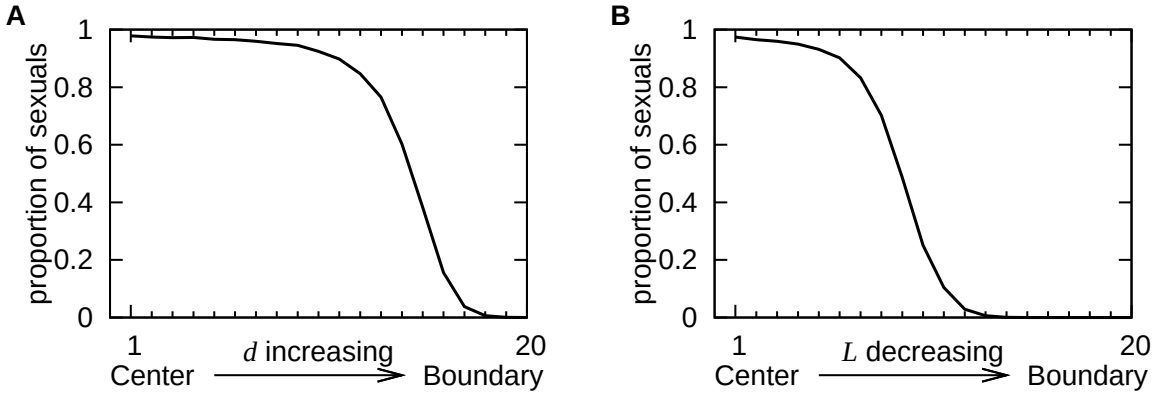



**Figure 3.2.:** Average equilibrium proportion of sexuals in the 20 patches with the patch index increasing from the center (1) to the boundary (20). The parameters that vary between patches are (A) the consumer death rate $d$, and (B) the number of different resources $L$. The death rate $d$ is increased in constant steps from 30 to 106, and the number of different resources $L$ is decreased from 256 to 66. The parameters that are not varied between patches are $d = 30$, $L = 256$. The remaining parameters are: regrowth percentage of resources $G = 20$, average number of initial individuals per patch $n = 50$, mutation rate per locus $\mu = 0.002$, sexual-to-asexual mutation rate $u = 0.001$, migration rate $\eta = 0.01$, and equal coupling strength to all 9 resources available to a genotype (i.e., $k = 0$).

and in the second graph (Fig. 3.2B) the number of different resources, $L$, was decreased from 256 to 66 with increasing patch index. In each case, the proportion of sexuals decreases from (almost) 100% to (almost) 0% with increasing patch index, i.e., with increasing harshness of the environment. The model thus reproduces the phenomenon of geographic parthenogenesis.

Fig. 3.3 also shows the average equilibrium proportion of sexuals in the 20 patches. In the first (Fig. 3.3A) and second graph (Fig. 3.3B) the percentage $G$ of consumed resource biomass that regrows between subsequent seasons is decreased from 40 to 11.5, together with a change in $d$ or $L$; and in the third (Fig. 3.3C) and fourth graph (Fig. 3.3D) the average number of initial individuals per patch $n$ is decreased from 58 to 20, together with a change in $d$ or $L$. Simultaneously varying two ecological parameters, the model again reproduces a pattern resembling geographic parthenogenesis in a proper parameter range.

These results are independent of the initial distribution of genotypes and modes of reproduction. We obtained the same graphs when we tested the following four initial situations: (a) 25 asexual and 25 sexual genotypes in random niches in each patch, (b) 50 sexual genotypes and no asexuals in random niches in each patch, (c) 25 sexual and 25 asexual genotypes in random niches in the first patch, with all other patches being empty, (d) 50 sexual genotypes in random niches in the first patch, with all other patches being empty. The first case imposes no bias towards one mode of reproduction, the second case shows the long-term effect of the rare production of asexual clones within sexual populations, the third and fourth case simulate the colonization of a new habitat by a population that initially displays either both modes of reproduction or reproduces only sexually.

The pattern of geographic parthenogenesis is robust against changes in other ecological factors, which are investigated in the following.

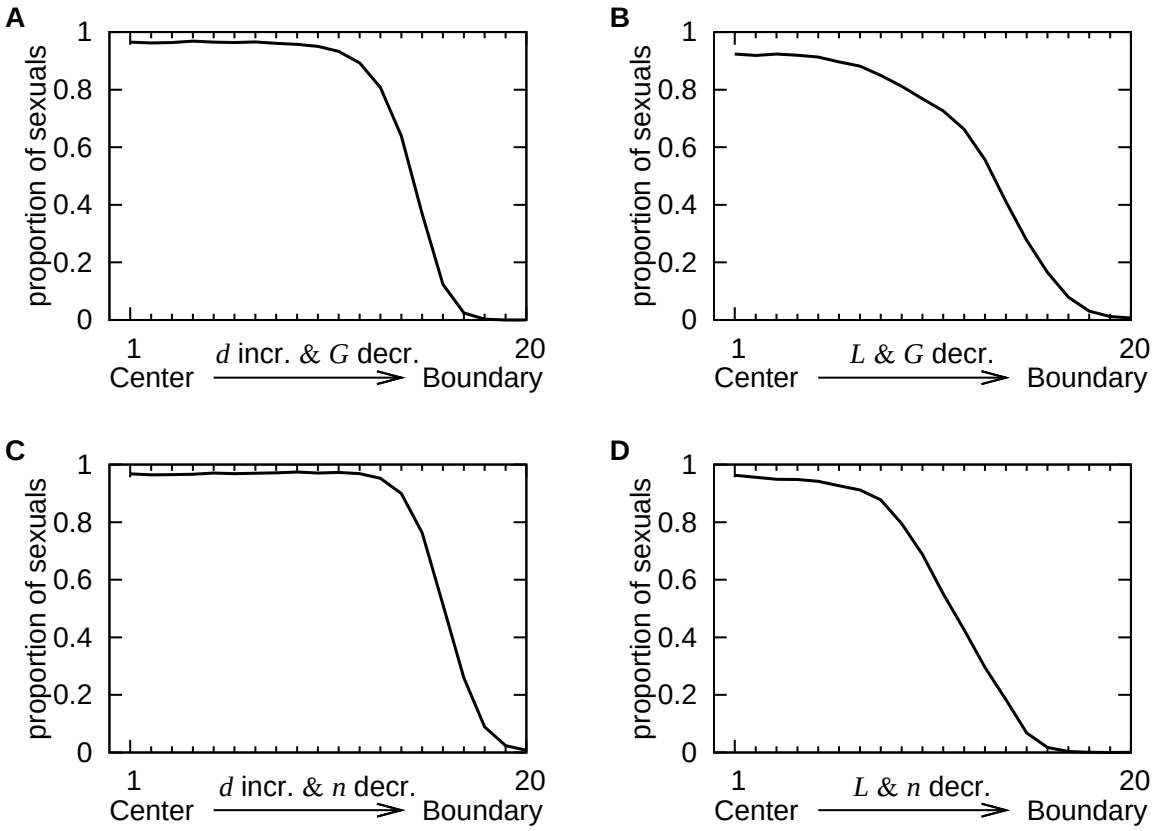



**Figure 3.3.:** Average equilibrium proportion of sexuals in the 20 patches with the patch index increasing from the center (1) to the boundary (20). The parameters that vary between patches are (A) the consumer death rate $d$ and the regrowth percentage of resources $G$, (B) the number of different resources $L$ and $G$, (C) the death rate $d$ and the average number of initial individuals per patch $n$, (D) $L$ and $n$. The death rate $d$ is increased in constant steps from 30 to 106, the number of different resources $L$ is decreased from 256 to 142, the regrowth percentage of resources $G$ is decreased from 40 to 11.5 and the average number of initial individuals per patch $n$ is decreased from 58 to 20 (the parameter intervals that contain the complete decline of sexual proportion from almost 100% fo almost 0%). The parameters that are not varied between patches are $d = 30$, $L = 256$, $G = 20$, $n = 50$. The remaining parameters are: mutation rate per locus $\mu = 0.002$, sexual-to-asexual mutation rate $u = 0.001$, migration rate $\eta = 0.01$, and equal coupling strength to all 9 resources available to a genotype (i.e., $k = 0$).

### 3.3.2 Influence of migration

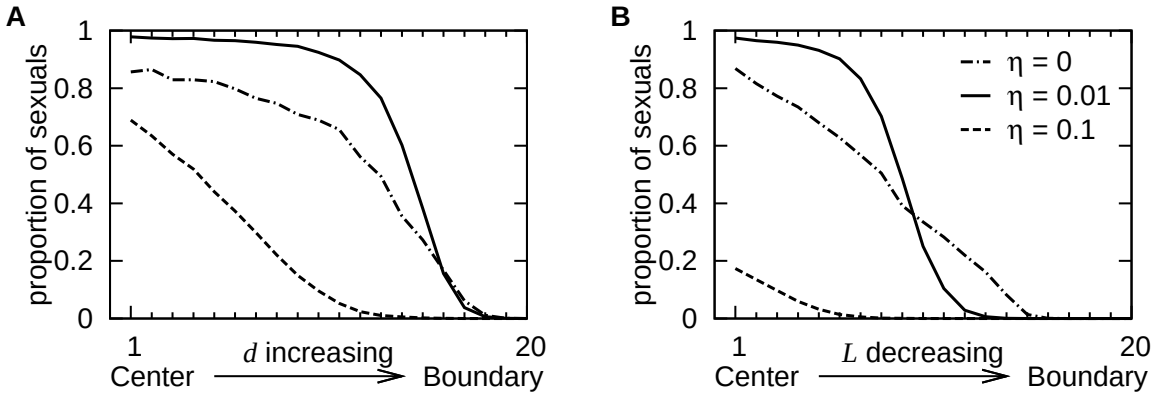



**Figure 3.4.:** Average equilibrium proportion of sexuals in the 20 patches with the patch index increasing from the center (1) to the boundary (20). The parameters that vary between patches are identical as in Fig. 3.2A and B, respectively, for three different values of the migration rate $\eta = 0$ (dot-dashed), $\eta = 0.01$ (solid), $\eta = 0.1$ (dashed). The parameters that are not varied between patches are $d = 30$, $L = 256$, $G = 20$, $n = 50$, $\mu = 0.002$, $u = 0.001$, $k = 0$.

Fig. 3.4 shows the influence of the migration rate $\eta$. The advantage of sexuals increases at first with increasing migration rate (Fig. 3.4A, the solid curve compared to the dot-dashed curve), because new genetic variance is brought in from neighboring patches, thus preventing a decline of genetic variance of the local sexual populations. However, in patches with low resource diversity (Fig. 3.4B) the advantage of sexuals decreases with increasing migration rate ($\eta = 0.01$), because the patches fail to provide diverse resources enhancing genetic variance of the sexual populations. When the migration rate becomes even larger ($\eta = 0.1$), the proportion of sexuals decreases more and more (Fig. 3.4A and B), because the asexual genotypes can be present in several patches at the same time, which decreases their extinction rate and enables them to benefit from the twofold cost per season incurred by the sexuals. We also investigated the case where migration happens before determining the genotypes of the individuals at the beginning of a new season (which can be interpreted as egg dispersal (Brendonck and Riddoch, 1999)). Here we found no significant changes in the behavior of the curves.

### 3.3.3 The impact of mutation rate per locus

In Fig. 3.5, $\mu$ is increased from the first to the last patch reflecting the fact that stressful environment can elicit a high mutation rate (Baer, 2007; Goho and Bell, 2000). In this case, the proportion of sexuals decreases from (almost) 100% to (almost) 0% with increasing patch index, i.e., with increasing environmental stress. When the mutation rate is high, the genetic variance of the asexual population is comparable with that of the sexual population. In this case, sexual reproduction makes no difference but the two-fold cost of producing males. Therefore, asexual reproduction dominates in harsh environments, while sexual reproduction dominates in favorable environment with less environmental stress, which is consistent with the phenomenon of geographic parthenogenesis.

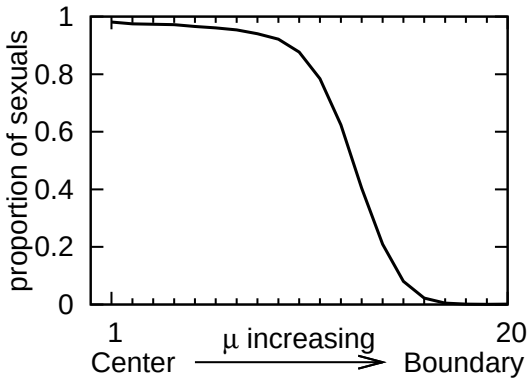



**Figure 3.5.:** Average equilibrium proportion of sexuals in the 20 patches with the patch index increasing from the center (1) to the boundary (20). The mutation rate per locus $\mu$ is increased from 0 to 0.019. The remaining parameters are: consumer death rate $d = 30$, number of different resources $L = 256$, regrowth percentage of resources $G = 20$, average number of initial individuals per patch $n = 50$, sexual-to-asexual mutation rate $u = 0.001$, migration rate $\eta = 0.01$, and equal coupling strength to all 9 resources available to a genotype (i.e., $k = 0$).

### 3.3.4 Gradient of ecological parameters results in pattern contradicting geographic parthenogenesis

We further investigated cases, where resources regrow fast or a considerable number of genotypes are present in a patch, i.e. one of the assumptions of the structured resource model with short supply (Scheu and Drossel, 2007) is not fulfilled. Fig. 3.6 shows the average proportion of sexuals in each patch that was obtained after 200 seasons, when an equilibrium had been reached. In the first graph (Fig. 3.6A), the regrowth percentage $G$ is decreased with increasing patch index, from 100 to 14.5; and in the second graph (Fig. 3.6B) the average number of initial individuals per patch $n$, is decreased from 130 to 16 with increasing patch index. Those choices of parameter intervals are made to represent the complete gradient of the sexual proportion from 0 to 100%. A decrease of the regrowth percentage $G$ without a simultaneous increase in the death rate or decrease in the number of the different resources (Fig. 3.6A), leads to an increase in the percentage of sexuals instead of a decrease. A large value of $G$ favors parthenogenetic reproduction, since there is no advantage of exploring new niches when resources grow very fast. A change of $n$ (either between patches or overall) does not qualitatively change our results, as long as $n$ is considerably smaller than $L$ even at the center, i.e., as long as there are enough unexploited niches that can be used by sexual offspring, and as long as $n$ is large enough to support a significant genetic variance. Otherwise, if $n$ is considerably large (Fig. 3.6B), i.e., most of the resources are exploited, there is no advantage for sexual offspring to be genetically different from their parents, hence asexual reproduction is dominant. Yet, with $n$ too small (Fig. 3.6B), the genetic variance in sexual population does not provide sufficient benefit to compensate the two-fold cost of sexuality. When the patches are isolated from each other, i.e., migration rate is zero, the consequence of small $n$ resulting in limited genetic variance in sexual population is more significant (Fig. 3.7B).

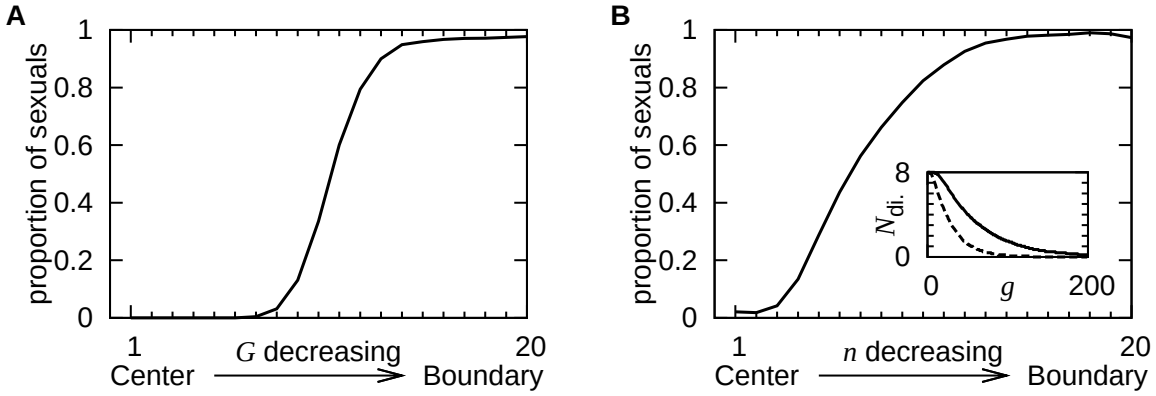



**Figure 3.6.:** Average equilibrium proportion of sexuals in the 20 patches with the patch index increasing from the center (1) to the boundary (20). The parameters that vary between patches are (A) the regrowth percentage of resources $G$, and (B) the average number of initial individuals per patch $n$. The regrowth percentage of resources $G$ is decreased from 100 to 14.5, and the average number of initial individuals per patch $n$ is decreased from 130 to 16. The parameters that are not varied between patches are $G = 20$, $n = 50$. The remaining parameters are: death rate $d = 30$, number of different resources $L = 256$, mutation rate per locus $\mu = 0.002$, sexual-to-asexual mutation rate $u = 0.001$, migration rate $\eta = 0.01$, and equal coupling strength to all 9 resources available to a genotype (i.e., $k = 0$). The inset in (B) shows the average number of diallelic loci $N_{\mathrm{di}}$ for a sexual population of average size $n = 50$ (solid) and $n = 25$ (dashed) at the beginning of each season as function of time. The curves are evaluated for a null-model, i.e., without interaction with resources. The mutation rate per locus is $\mu = 0$. The curves for a parthenogenetic population are identical with those for a sexual population of the same size.

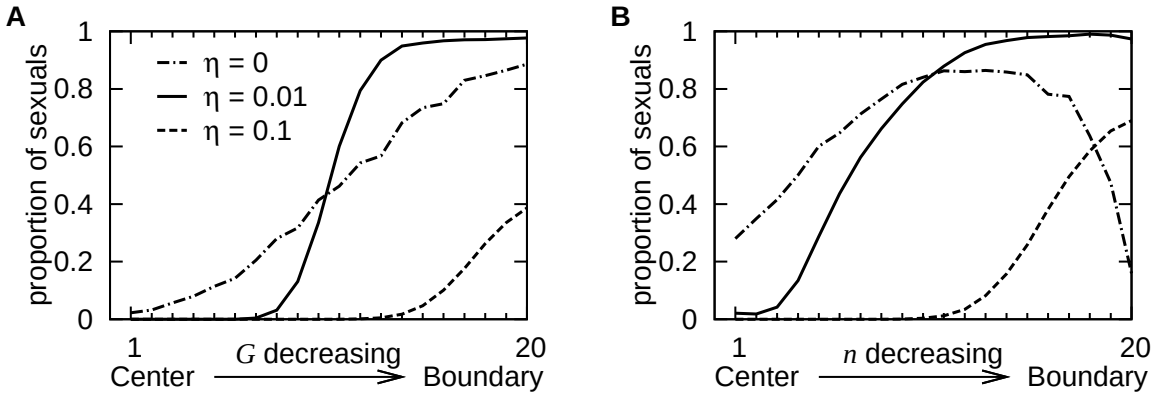



**Figure 3.7.:** Average equilibrium proportion of sexuals in the 20 patches with the patch index increasing from the center (1) to the boundary (20). The parameters that vary between patches are identical as in Fig. 3.6A and B, respectively, for three different values of the migration rate $\eta = 0$ (dot-dashed), $\eta = 0.01$ (solid), $\eta = 0.1$ (dashed). The parameters that are not varied between patches are $d = 30$, $L = 256$, $G = 20$, $n = 50$, $\mu = 0.002$, $u = 0.001$, $k = 0$.

Fig. 3.7 shows the influence of the migration rate $\eta$ on the geographic distribution of sexual reproduction, while the regrowth percentage of resources $G$ (Fig. 3.7A) or the average number of initial individuals per patch $n$ (Fig. 3.7B) decreases with increasing patch-index. In patches with large values of $G$ or $n$, genetic diversity is not promoted, neither is sexual reproduction. The proportion of sexuals decreases with increasing migration rate (Fig. 3.7), since migration helps asexual clones occupy niches in other patches and gain more resources. In patches with small values of $G$ or $n$, i.e., when the assumptions of the original structured resource model (Scheu and Drossel, 2007) are fulfilled, the proportion of sexuals increases at first with increasing migration rate (Fig. 3.7), because new genetic variants are brought in from neighboring patches, thus preventing a decline of genetic variance of the local sexual populations. When the migration rate becomes even larger, the proportion of sexuals decreases more and more (Fig. 3.7), because asexual populations gain many resources via migration to a new patch, which enormously reduces the advantage of sexual offspring able to efficiently exploit different resources from that of their parents.

### 3.3.5 Alternative genetic implementations

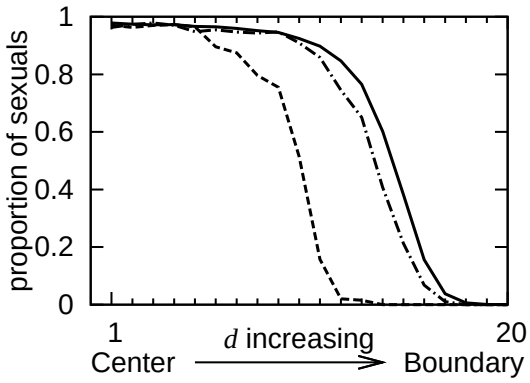



**Figure 3.8.:** Average equilibrium proportion of sexuals in the 20 patches with the patch index increasing from the center (1) to the boundary (20). The parameters that remain constant between patches are identical as in Fig. 3.2A, except for $k$ which determines the coupling strength between consumer and resources whose genotype differs in one bit from the genotype of the consumer, $e^{-k}$. The parameter that varies between patches is the death rate $d$ increasing from 30 to 106 for $k = 0$ (solid), from 30 to 68 for $k = 0.5$ (dot-dashed), from 20 to 58 for $k = 1$ (dashed). The choices of parameter intervals are made to represent the complete gradient of the sexual proportion from 0 to 100%.

We investigated the effect of a different coupling strength to neighboring resources (Fig. 3.1). For $k = 0.5$ or 1 (Fig. 3.8), the parameter region where sexual reproduction dominates becomes different from that for $k = 0$, since a larger $k$ has a similar effect as a larger $d$ (Eq. (2.1) with the coupling strength to neighboring resources $\alpha = e^{-k}$). Yet geographic parthenogenesis is also observed. When the number of resources on which a genotype can feed is extended to a larger neighborhood, there is no longer any advantage of sexual reproduction, because there are no unexploited resources left even for smaller values of $n$. We also varied the number of loci. When we performed our simulations with 9 loci and up to $L = 512( = 2^9)$ different

resources, the parameter interval where sexual reproduction dominates became larger. With 5 or less loci, we could not obtain a proportion of sexuals close to 1, since the difference in genetic variance between sexual population and asexual population is insignificant. With 7 loci and up to $L = 128(= 2^7)$ different resources, we could obtain results similar to those with 8 loci only with sufficiently large $k$, i.e. when an individual could not feed on neighboring resources. With smaller $k$, each genotype would be able to exploit 8 resources (1 plus 7 neighboring resources, see Fig. 3.1 with 7 loci), which is 1/16 of all resources. In order to have unused resources that could be exploited by the sexual offspring, the population size would have to be very small - and then the genetic variance would be lost so quickly that sexuals have no advantage. With 6 loci, the parameter range in which we found a dominance of sexual reproduction was much smaller.

To prove that the result of the model is independent of the genetic implementation, two versions of the structured resource model with alternative genetic implementations are investigated in addition.

### Explicit genetic with additive trait values

We now use two traits (use more than two traits works too, but the results shown below are obtained with two traits), each of which is determined by 20 diallelic loci (values 0 and 1), which contribute additively to the trait value. Thus, each trait has 21 possible values (0,1,...,20). Therefore, there are $L = 21 \times 21$ different resources in a patch. The coupling coefficient to the resources is 1 if the traits match exactly that of the resources, $e^{-1}$ if they differ by 1 in one trait, $e^{-2}$ if they differ by 1 in both traits, and zero otherwise.

When sexual offspring is produced, for each of the 20 loci one to two cross-over points are randomly chosen for recombination. Because this version of the model is more likely to loose genetic variance (by loosing alleles) than the others, we have to use a larger number of patches. In nature, the arrangement of patches is two-dimensional anyway, and the number of patches is large, so this change in our model is realistic (but costs much more computer resource.) Fig. 3.9 shows the prevalence of sexual reproduction over a wide range of death rate values and geographic parthenogenesis with this alternative genetic implementation.

### Explicit genetic with spatial constraint

In the versions of the model mentioned so far, we assume that each offspring is placed into a patch and assigned to a niche with the trait value that matches its own. Each offspring can therefore feed on its best adapted resources and the neighboring resources.

Now, we introduce a version where each offspring is placed into an arbitrary niche and solely replies on the resource that is present there. We assume that each genotype is able to feed on each resource, but with an efficiency that depends on the similarity between the trait value of its genotype and the trait value of the niche. The coupling coefficient $\alpha$ of an individual is now set to be 1 for resources that have the same trait values as the individual or are only different at one trait, otherwise the interaction coefficient is set to be 0.3. (Other values work also, but these are the values used for the simulation presented in the Fig. 3.10.)

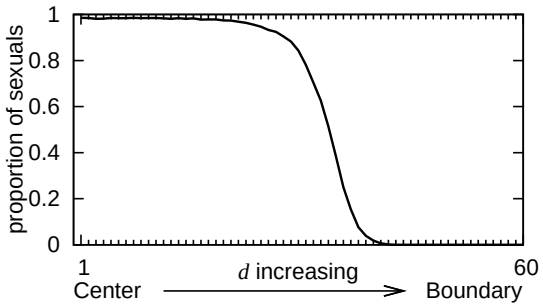



**Figure 3.9.:** Average equilibrium proportion of sexuals in the 60 patches with the patch index increasing from the center (1) to the boundary (60). The parameter that varies between patches is the consumer death rate $d$. The death rate is increased in constant steps from 20 to 138. The parameters that are not varied between patches are $L = 21 \times 21$, $G = 30$ ($R_{\max} = 300$), $n = 70$, mutation rate per locus $\mu = 0.0002$, sexual-to-asexual mutation rate $u = 0.0001$, migration rate $\eta = 0.01$. (Averaged over 1000 simulations.)

We choose the same genetic makeup as described in the Section 3.2 (i.e., 8 diallelic loci). In contrast to the model presented there, we now use larger population sizes (because only a small part of individuals are placed in the correct niche) and a larger maximum resource biomass (so that an individual can multiply sufficiently between the beginning and end of a season, resulting in different numbers of offspring dependent on the coupling coefficient). Besides, we now introduce a decline in maximum resource biomass toward the "north" and a fixed season duration. This latter change is more realistic than the other models presented so far, and it is required in this version in order to avoid that each individual eats until all resources are consumed. Fig. 3.10 shows again the prevalence of sexual reproduction over a wide range of death rate values and geographic parthenogenesis, while the death rate increases with increasing patch index, imitating the transition from favorable to harsh environment.

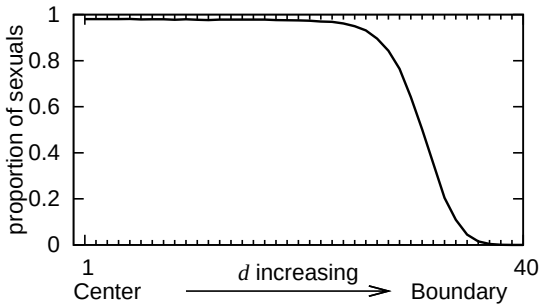



**Figure 3.10.:** Average equilibrium proportion of sexuals in each patch with the patch index increasing from the center (1) to the boundary (40). The parameter that varies between patches is the consumer death rate $d$. The death rate is increased in constant steps from 20 to 176. The maximum of resource size is decreased in constant steps from $R_{\max} = 10^6$ to $7.153 \cdot 10^5$. The parameters that are not varied between patches are $L = 256$, $G = 10\% \cdot R_{\max}$, $n = 1422$, mutation rate per locus $\mu = 0.0002$, sexual-to-asexual mutation rate $u = 0.0001$, migration rate $\eta = 0.01$. (Averaged over 1000 simulations.)

## 3.4 Analysis

In order to understand the simulation results from the structured resource model in greater depth, we first consider the case of a single patch (or, equivalently, a set of isolated patches). Due to the twofold cost of producing males incurred once per season, sexuals can only have an advantage when there is sufficient genetic variance in the patch so that offspring can be generated that are capable of exploiting unused resources. We therefore evaluate in the following the genetic variance of sexuals and asexuals under different conditions. If there was no selection, the genetic variance would be independent at each locus and fully determined by drift. With a population size of $n$ and an initial proportion of 50 percent of each of the two alleles at each locus, the probability of not having lost one of the two alleles after $g$ seasons can be estimated to be roughly of the order $e^{-g/n}$ (since the number of individuals with a given allele changes per generation by the order of $\sqrt{n}/2$, and since the number of random steps of this size required to cover the distance $n/2$ is of the order of $n$). One can therefore expect the number of loci with two alleles to become very small within 100 seasons.

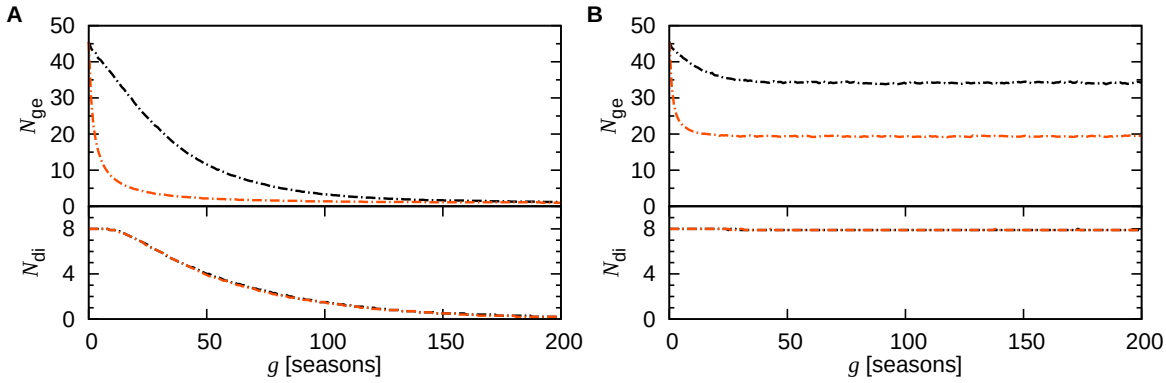



**Figure 3.11.:** Average number of diallelic loci $N_{di}$ and genotypes $N_{ge}$ for a sexual (black lines) or parthenogenetic population (red lines) of average size $n = 50$ at the beginning of each season as function of time. The graphs are evaluated for a null-model, i.e., only with drift and without selection, and the two reproductive modes are considered independently from each other. The mutation rate per locus is (A) $\mu = 0$ and (B) $\mu = 0.016$. The average number of diallelic loci evolves in the same way for both sexual and parthenogenetic reproduction.

This is indeed the case, as shown in Fig. 3.11. Without mutations, the genetic variance eventually declines to zero (Fig. 3.11A). We performed the simulation once for a purely sexual population and once for a purely asexual population, without taking into account selection, i.e., with each individual having the same chance of being the parent of a child in the next season. While the number of diallelic loci behaves exactly in the same way in both cases, the number of genotypes is considerably larger for the sexuals, due to recombination. When the mutation rate is nonzero (Fig. 3.11B), the genetic variance reaches a nonzero stationary value. As long as the mutation rate is small, the sexuals have a clear advantage over the asexuals in terms of genetic variance. A single mutation in a sexual individual at a locus that has lost one of the two alleles can generate many new genotypes through recombination with all the other genotypes. In contrast, a mutation in an asexual individual generates only one new genotype. If the mutation rate is higher, this advantage of the sexuals becomes smaller. Fig. 3.11B shows the result obtained

with $\mu = 0.016$, where the number of sexual genotypes is less than twice the number of asexual genotypes, which means that the two-fold cost of sex cannot be compensated (remember that this simulation was performed without taking into account differences in resource availability). Therefore, the patches with high mutation rate $\mu$ are dominated by parthenogenetic reproduction (Fig. 3.5).

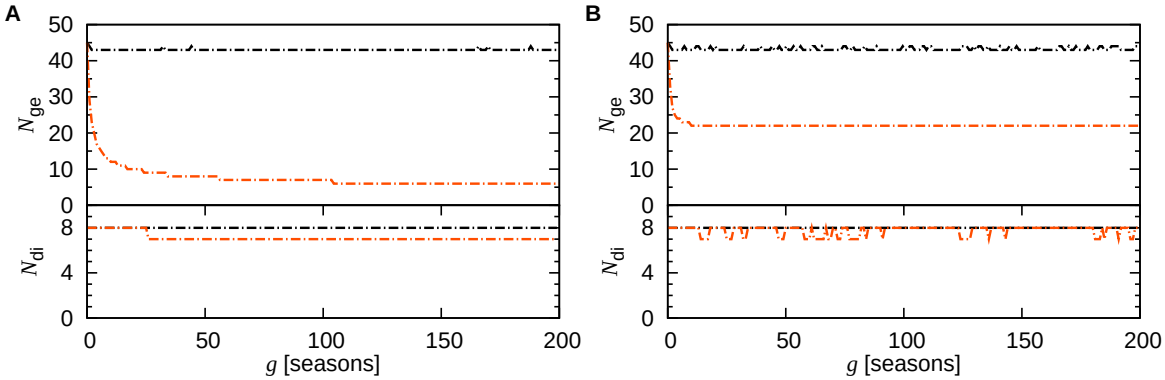



**Figure 3.12.:** Same as Fig. 3.11, but with resource dynamics. The additional parameters are: death rate $d = 30$, number of different resources $L = 256$, regrowth percentage of resources $G = 20$, average number of initial individuals per patch $n = 50$, and equal coupling strength to all 9 resources available to a genotype (i.e., $k = 0$).

When resource dynamics are taken into account, rare alleles will in fact have a considerable advantage in sexual species due to being able of exploiting unused resources. The loss of an allele becomes therefore less likely. This is shown in Fig. 3.12A and Fig. 3.12B for a zero and a nonzero mutation rate, respectively. A comparison with Fig. 3.11 demonstrates a large difference between sexuals and asexuals: Even without mutation, the sexuals usually lose none of their alleles, because rare alleles can recombine with other genotypes to exploit underutilized resources. Mutation does not confer an additional advantage. In contrast, the number of asexual genotypes depends strongly on the mutation rate. Nevertheless, just as for the sexuals, resource dynamics prevents the loss of rare alleles. Although individuals of an asexual lineage that had plenty of food in the previous season lay many eggs, they produce offspring that feed all on the same (limited) resource in the present season. At the end of the season the number of individuals of this genotype is approximately the same as when there initially had only been one individual. More individuals of the same genotype at the beginning of the season thus do not lead to a larger number of individuals at the end of the season. The total number of asexual genotypes decreases in the absence of mutations to a single-digit number because of gene drift. Presence of similar genotypes results in overlaps of niche use. Individuals of similar genotypes compete for the same resources, and are therefore disadvantaged. Without recombination and mutation the number of different genotypes declines until the remaining individuals have (almost) no overlap in resource use.

Finally, we evaluate the number of loci $N_{di}$ for which both alleles are present in the population, and the number of different genotypes $N_{ge}$ for the full model for the simulation parameters of Fig. 3.4A. As shown in Fig. 3.13, the sexuals quickly lose their genetic variance in patch number 20, where death rate is high, and where asexuals have the advantage of having more offspring. On the other hand, the sexuals can maintain their genetic variance in the first patch,

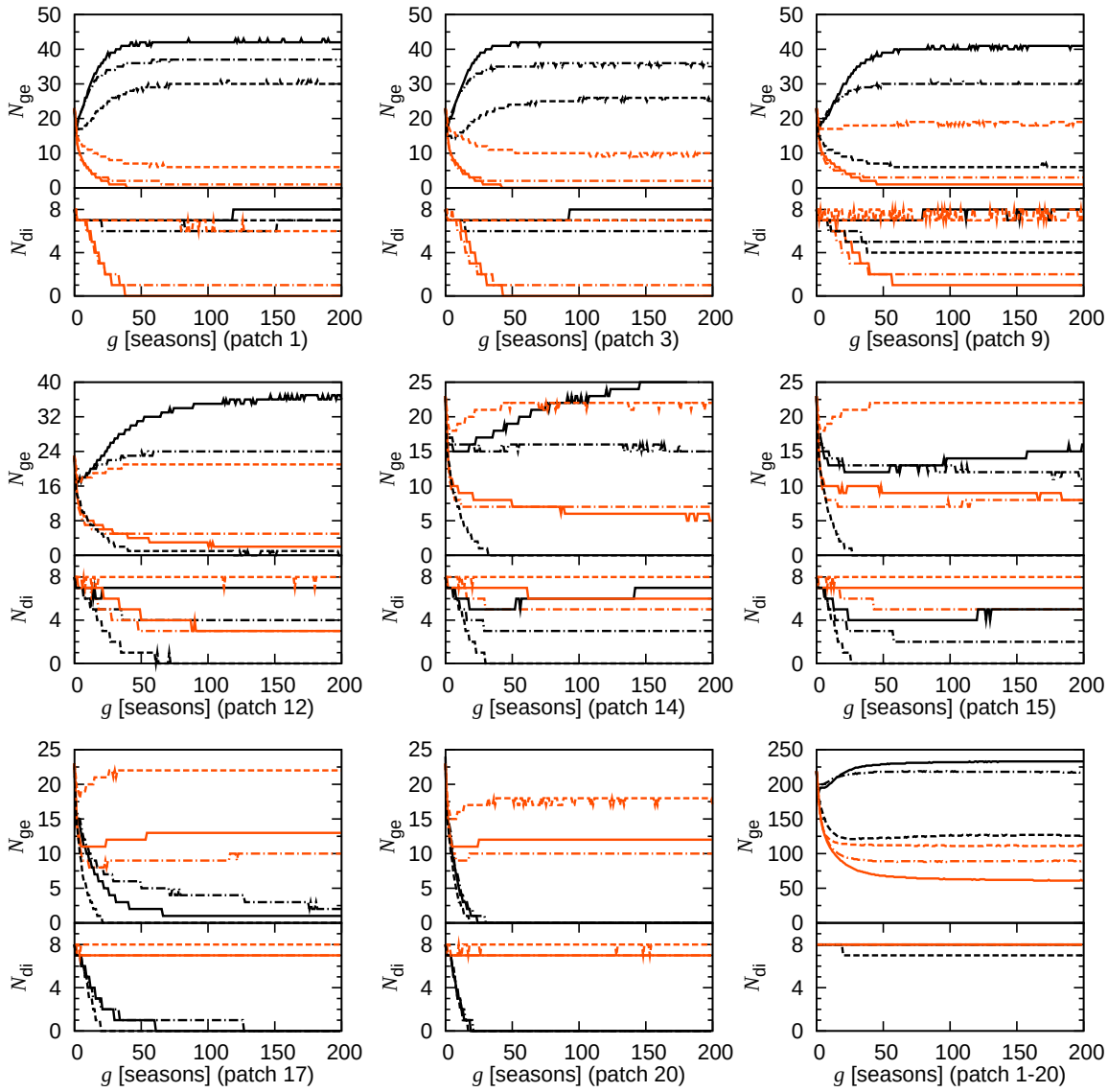



**Figure 3.13.:** Average number of loci $N_{di}$ with two alleles and of different genotypes $N_{ge}$ for a situation where sexual (black lines) and parthenogenetic reproduction (red lines) compete with each other, as function of time. The simulations were performed for the parameter set of Fig. 3.4A, i.e., $L = 256$, $G = 20$, $n = 50$, $\mu = 0.002$, $u = 0.001$, $k = 0$ and death rate $d$ increasing in constant steps from 30 to 106. Dot-dash line: $\eta = 0$; solid lines: $\eta = 0.01$; dash line: $\eta = 0.1$. (The plots of unselected patches show no qualitative changes in the behavior of the curves in comparison with the plots of their neighboring patches.)

where they succeed at producing more offspring than the asexuals, due to being capable of utilizing more resources. In both cases, the winning mode of reproduction can already be identified during the first few season, due to the rapid decline of the other mode of reproduction. This means that in favorable environments sexual reproduction is not only a long-term advantage, but also a short-term advantage.

Fig. 3.13 shows that migration can further increase the genetic variance of sexuals as long as the migration rate is not too large. Interestingly, over the entire set of patches, almost all alleles are present irrespective of the mode of reproduction ($N_{\mathrm{di}}$ in the last graph of Fig. 3.13). This proves once again that structured resources prevent the decline of genetic variance in general, by preferring rare alleles.

## 3.5 Discussion

In this chapter, we have modified and extended a mathematical model for sexual reproduction that is based on a broad spectrum of limited resources that regrow slowly (Scheu and Drossel, 2007), in order to obtain the phenomenon of geographic parthenogenesis. In this model, the number of genotypes that can coexist at the same place is limited, thus providing an advantage to sexuals whenever the offspring can acquire a genotype that enables it to exploit unused resources. In contrast to the original model (Scheu and Drossel, 2007), which was based on quantitative genetics, we now use a genetically explicit model. This permits us to generate sexual offspring via recombination, and to explicitly evaluate the number of different alleles present in the populations. The two different implementations used in the two models, represent two limiting cases: The quantitative genetic model includes only two parameters to specify a resource and a genotype, both of which are continuous and Gaussian distributed with a constant genetic variance, which implies that they result from the superposition of the effects of many genes that contribute additively to it. The genetically explicit model uses eight parameters to specify a resource and a genotype, with each parameter taking only two values. Both genetic implementations lead to a prevalence of sexual reproduction when there is a sufficient amount of unexploited resources and when the ability to exploit these resources leads to an increase in the number of offspring. This demonstrates that the outcome of the model is sufficiently generic and does not rely on the precise way in which genetics is implemented. If only the following three requirements are met, sexual reproduction can prevail over a wide parameter range: (i) the number of locally coexisting genotypes is so small that they can use only part of the resources with good efficiency. (ii) Sexual parents can have offspring that can efficiently use resources that their parents could not efficiently use. (iii) Resources regrow slowly.

One can imagine various other variants of the model that satisfy these requirements when parameter values are chosen in an appropriate range. For instance, we performed simulations of a genetically explicit version of the quantitative genetic model, where each trait value resulted from the addition of the values at 20 diallelic loci. This version of the model displays similar results when there is a sufficiently large number of patches that are coupled by migration, so that alleles do not get lost too quickly. We also performed simulations with a fourth version of the model: Instead of letting each individual feed on the resource(s) it is best adapted to, we placed each individual directly into a niche, where it could feed with an efficiency that depends on the extent of agreement between the trait value of the individual and the niche value. This version

of the model permits using much larger population sizes, since only part of the individuals feed with maximum efficiency. It again displays the prevalence of sexual reproduction.

While we have demonstrated this pattern of geographic parthenogenesis by using the quantitative genetic model (Chapter 2), it occurs also for the genetically explicit model and the other modifications mentioned in the previous paragraph (see Section 3.3.5 for more information), when patches are arranged in a similar way. We have thus found a class of models that can produce the phenomenon of sexual reproduction and the phenomenon of geographic parthenogenesis by exactly the same mechanisms.

We have explained the results of the computer simulations by considering the genetic variance of the sexuals as function of the parameters. Whenever recombination, mutation and migration together allow for many more sexual than asexual genotypes, sexual reproduction wins over parthenogenetic reproduction when resources are scarce, despite the twofold cost of males that sexuals incur once per season.

The model used in here, of course, is only a simplified description of sexual reproduction in a spatially inhomogeneous environment. In the simulations, we used 20 patches with up to 256 different resources each, and the consumers were represented by a genotype of 8 bits and an average population size of 50, which can barely capture the extent and importance of overall spatial variation and local restriction of resources and consumer genotypes. Nevertheless, the model demonstrates nicely the advantage of sexual reproduction wherever it enables consumers to exploit the resources more efficiently, and the transition to parthenogenesis wherever there is no advantage of consumers switching to other resources.

Other theories for the evolution of sex cannot easily be extended to generate geographic parthenogenesis. Contrary to geographic parthenogenesis, lottery models (Williams, 1966) predict that sexual reproduction is favored at the boundary of a species' range, where the habitat is capricious and unpredictable. A spatially extended model by Salathé *et al.* (2006), which is based on Muller's ratchet decreasing the fitness of asexuals while they invade a sexual population, predicts the dominance of asexuals in marginal habitats, with small populations that can be invaded rapidly. However, such an asexual invader could persist only temporarily, until its fitness has decreased to the point where it dies out or a sexual invader replaces it again. Geographic parthenogenesis therefore cannot be an equilibrium phenomenon in that model. Models based on the Red Queen mechanism (Hamilton, 1980; Jaenike, 1978) require a decreasing impact of parasites on their host towards the boundary of the host's range in order to produce geographic parthenogenesis. Such models require assumptions about how host and parasite change with the geographic location (Lively, 2001). Indeed, hosts are more likely to be exposed to a larger number of parasites in the center of their range which weakens the Red Queen mechanism (Kouyos *et al.*, 2009) and therefore the advantage of sexual reproduction. Further, Howard and Lively (1994) demonstrated that a model that only includes the effect of parasites reducing the fitness of the host, is not sufficient to explain the maintenance of sex. Finally, many mathematical models on the maintenance of sexual reproduction are based on population genetics (Martin *et al.*, 2006; Otto, 2009), where fitness values are assigned to genotypes. Since such models do not explicitly consider the ecological environment, there is no straightforward way to extend them to explain geographic parthenogenesis. Overall, processes such as Muller's ratchet, interaction with parasites, and interactions between genes, may all affect the mode of reproduction. However, resources are fundamental and universal, no living organism can sur-

vive or even reproduce without resources. The structured resource model including a broad spectrum of limited resources, together with stochastic effects (drift) is unique in providing a generally satisfying explanation for the phenomenon of geographic parthenogenesis and for the general dominance of sexual reproduction.

This model is limited by the fact that it is based on equilibrium dynamics and therefore does not take into account the ever continuing change of the biotic and abiotic environment. The set of resources used here is the same in every patch and over the duration of the simulation. Recent work on the advantages of sexual reproduction (Morran *et al.*, 2009; Otto, 2009) focuses more on the ability of sexually reproducing organisms to adapt to new challenges. A combination of these approaches with an explicit modelling of structured resources could be an important step towards a synthesis of the different theories of evolution and maintenance of sex.

The structured resource model, tailored to short-lived organisms, is now proven available to explain the maintenance of sex with four different genetic implementations. With an additional spatial extension it even produced a pattern resembling geographic parthenogenesis. These achievements evidence the explanatory power of the Tangled Bank hypothesis that inspired this mathematical model.

# Part II.
# Long-lived organisms

# 4 Life histories and Cope's rule from an explicit consumer-resource model based on metabolic theory

As the preliminary work for the study shown in the next chapter, we explore the consequences of metabolic theory for life histories and life history evolution. We use a mathematical model for an iteroparous species[i] and its resources, taking into account the allometric scaling of consumption, metabolism and mortality with consumer body mass. Mortality is assumed to be density dependent, and the dynamics of resources are explicitly modelled. We find that in populations that use more or faster growing resources the individuals have a shorter life span and a higher mortality, and that individuals in populations with a larger adult body mass have a longer lifespan, a larger number of offspring per female and a higher biomass density. When we allow the adult body mass to evolve, it increases in time without limits. When we allow the offspring body mass to evolve, it becomes smaller. Both trends result from the allometric scaling of mortality and are kept in limits by trade-offs other than those included in our model.

## 4.1 Introduction

The life history of an organism is affected by trade-offs that are due to a limited energy budget. There are for instance trade-offs between growth in body mass and reproduction, between offspring number and offspring mass, between reproduction and survival, and between present and future reproduction (Stearns, 1992). Life histories are shaped by natural selection during biological evolution. Life history theory presupposes that life cycles are optimized to achieve the largest population growth rate, $r$ (measure of fitness, see p.15). The equation used to determine the maximum growth rate is the Euler-Lotka equation (Euler, 1760; Lotka, 1907). Thereby, it is assumed that the number of newborn offspring changes exponentially with the year, i.e.,

$$N_{t,0} = e^{rt} N_{0,0}\,,$$

where $N_{t,0}$ denotes the number of newborn offspring in year $t$. The number of individuals in age class $X$ is the number of offspring $N_{t-X,0}$ that were born $X$ years ago multiplied by the probability $l(X)$ that a newborn survives to age class $X$: $N_{t-X,0}l(X)$. The number of individuals in all age classes is $\sum_{X'} N_{t-X',0}l(X')$. The proportion of individuals in age class $X$ is thus

$$\frac{N_{t-X,0}l(X)}{\sum_{X'} N_{t-X',0}l(X')} = \frac{e^{r(t-X)}N_{0,0}l(X)}{\sum_{X'} e^{r(t-X')}N_{0,0}l(X')} = \frac{e^{-rX}l(X)}{\sum_{X'} e^{-rX'}l(X')}\,.$$

When the number of individuals in a population is constant, i.e., the maximum growth rate $r$ is zero, this proportion is

$$\frac{l(X)}{\sum_{X'} l(X')}\,.$$

[i] **Iteroparous** in Glossary.

A limited population at equilibrium is thus in stationary age distribution.

The main challenge in life history theory consists in obtaining realistic estimates of the functions $l(X)$ and $m(X)$[ii], or equivalently of the elements of the so-called Leslie matrix (Leslie, 1945). Usually, they are postulated on the basis of plausible scenarios and empirical knowledge.

Recently, it has been emphasized that metabolic theory has profound implications on the evolution of life histories (Brown and Sibly, 2006). Larger organisms have a lower rate of production per unit body mass, and they have a lower mortality (Brown *et al.*, 2004; Ernest *et al.*, 2003). While metabolic theory is now taken into account in food web models (Rall *et al.*, 2008), it has not yet been used to obtain life histories and life history evolution based on the dynamics of consumers and their resources. The only exception is the paper by Kawecki (1993), who considers consumers exploiting resources in a patch with the consumption rate and maintenance cost depending on body mass. The consumers may adopt different strategies for investing in growth and in offspring production. Which strategy has the highest fitness depends on the total amount of resources in the patch and on the other strategies present. The model shown in this chapter differs also in other respects from the classical life history approaches. Instead of performing an optimization calculation this model explicitly includes the dynamics of resource exploitation and the competition for resources between populations with different reproductive strategies. As has been pointed out by Stearns (2000), approaches of this type to life history theory are very much needed.

Here, we derive for the first time life history traits from a full dynamical model for a consumer species and its resource, taking into account metabolic theory, which determines the scaling of consumption, metabolism and mortality with the body mass of the consumer. The consumer population size is limited by a density dependent term, and consequently the population becomes stationary after some time. We evaluate various life history parameters in the stationary population. Furthermore, we perform an evolutionary simulation by introducing into the population individuals with a different body mass at maturity. We find that body mass evolves towards larger values. This means that Cope's rule (Hone and Benton, 2005) follows from metabolic theory alone, without need to take into account additional advantages of larger body size such as the ability to exploit new niches or to avoid predators more efficiently.

## 4.2 Model

Our model is an individual-based model for iteroparous species. After birth, individuals grow due to consuming resources, they loose mass due to respiration, and once a year they produce offspring if their body mass is above a threshold value. The probability of dying depends on body mass and density. Resources have a logistic growth, and they are reduced due to consumption. Our consumer-resource model is similar to the one used by Rall *et al.* (2008), which is based on the work of Yodzis and Innes (1992) and was updated with new allometric coefficients (Brown *et al.*, 2004; Ernest *et al.*, 2003). Since an individual dies as a whole and not partially, mortality is implemented as a probability for occasional death in our individual-based model. We assume that the number of males and their fecundity do not limit the population growth

[ii] $m(X)$: the average clutch size of individuals in age class $X$. (Stearns, 1992)

rate, i.e., including males makes no significant difference apart from making the equation more complicated. Therefore, we consider only females as in other treatments of life history theory (Stearns, 1992).

The model is initiated with a maximum resource biomass $R = K_\mathrm{r}$. The area of the living space is chosen as unit, thus resource biomass and biomass density have the same value. The body mass of the resources is set to be unit as a further simplification, and the resource biomass $R$ of the resource population is thus equal the population size. Resource population grows continuously according to the logistic function[iii] with a maximum growth rate $G$ and lose biomass due to being consumed, i.e.,

$$\dot{R} = G\left(1 - \frac{R}{K_\mathrm{r}}\right)R - \sum_{i=\text{consumers}} \xi_i \varepsilon B_i F \,, \tag{4.1}$$

where $F$ is the functional response[iv] and the sum is taken over all consumer individuals. The body mass $B_i$ of consumer $i$ increases from the initial value $B_\text{juvenile} = 1$ due to feeding and respiration according to the equation

$$\dot{B}_i = -\xi_i B_i + \lambda \xi_i \varepsilon B_i F \,. \tag{4.2}$$

The ecological efficiency $\lambda$ was chosen to be $0.4$ (Turner, 1970), and the maximum consumption rate $\varepsilon$ of the consumers relative to their metabolic rate is a parameter of the model. Consumer individuals eat resources according to a Holling type II functional response (Holling, 1959),

$$F = \frac{R/K_\mathrm{r}}{1 + R/K_\mathrm{r}} \,. \tag{4.3}$$

Since the handling time is thereby taken to be unit, the equation has the form of the Monod equation (Healey, 1980). The consumers loose weight due to metabolism

$$\xi_i = a B_i^{-0.25} \,. \tag{4.4}$$

The allometric constant $a$ is chosen to be 0.314, which is a typical value for consumers of resources with unit body mass (Rall *et al.*, 2008). Larger individuals need less energy per body

[iii] **Logistic function** or logistic curve is used to describe the growth of population in an area of fixed limits (Pearl and Reed, 1920). The function can be written in the form (Lloyd, 1967)

$$R = \frac{K_\mathrm{r}}{1 + e^{d - Gt}} \,,$$

and its time derivative is then

$$\dot{R} = G\left(1 - \frac{R}{K_\mathrm{r}}\right)R \,,$$

where $G$ is the maximum mass-specific growth rate, and $K_\mathrm{r}$ is the maximum resource biomass.

[iv] **Functional responses** describe the relationship between an individual's rate of consumption and food density. They have generally been divided into three types. - http://www.tiem.utk.edu

mass for metabolism. The parameters in the functional response are chosen such that $R/K_r$ cannot be close to 0 in the stationary state of Eq. (4.1). Otherwise, the consumers would not be able to survive.

When an individual does not obtain enough food, its body mass may drop below the minimum juvenile mass $B_{\text{juvenile}}$, in which case the individual is removed from the system.

A year has the duration $\tau = 1$. In order to efficiently implement the mortality of individuals, each year is divided into $f_{\text{selection}} = 10$ time intervals of equal length. At the end of each time interval every individual dies with a probability $p_i \in [0, 1]$ depending on its body mass $B_i$ and the total biomass of all consumers in the system, $\sum_l B_l$:

$$p_i = 1 - e^{-\chi_i}, \quad \text{with } \chi_i = \frac{1}{n} \sum_{l=\text{consumers}} B_l / B_i^{0.25} \tag{4.5}$$

This is the time-discrete version of a density dependent mortality, such as for instance implemented in Kartascheff *et al.* (2010). Larger individuals have a lower mortality. A scaling of the mortality with $B_i^{-0.25}$ means that the dominant causes of death affect the biomass of an age class in a similar way as metabolism does. This type of scaling is also supported by empirical data (Brown *et al.*, 2004). The parameter $n$ is related to the maximum biomass imposed by the limited space of the system. Dead individuals are removed from the system.

Once a year, reproduction takes place. We assume that a female is sexually mature once it reaches the minimum adult body mass $B_{\text{adult}}$. Females with a body mass $B_{\text{mother,prev}}$ larger than $B_{\text{adult}}$ by at least twice $B_{\text{juvenile}}$ produce

$$c = \frac{B_{\text{mother,prev}} - B_{\text{adult}}}{2 \cdot B_{\text{juvenile}}} \tag{4.6}$$

offspring (rounded to an integer) with body mass $B_{\text{juvenile}}$ (= 1 except in the evolutionary model briefly described later in Section 4.3.2). Taking into account parental care such as nursing and feeding, we estimate the cost of each offspring to be twice $B_{\text{juvenile}}$. Therefore, the body mass of the mother after offspring production becomes

$$B_{\text{mother, after}} = B_{\text{mother, prev}} - 2 \cdot B_{\text{juvenile}} \cdot c\,. \tag{4.7}$$

The offspring body mass $B_{\text{juvenile}}$ is the minimum juvenile body mass after parents have stopped investing into their offspring, i.e. when the juveniles begin to independently feed on resources.

## 4.3 Results

In the following we will explore the influence of five parameters (the maximum consumption rate $\varepsilon$, the intrinsic growth rate of resources $G$, the maximum biomass of resources $K_r$, the density limiting factor $n$ and the minimum adult body mass $B_{\text{adult}}$) on life history traits such as age at maturity, mean generation time, expected life time, probability of surviving from birth to beginning of age class $X$, expected number of offspring for a female in age class $X$ and fecundity for a female in age class $X$. The parameters and life history traits are listed in

**Table 4.1.:** Meaning of Symbols used in the model

| Symbol | Meaning |
|---|---|
| $\tau$ | a year's time |
| $f_{\text{selection}}$ | number of selections per year |
| $B_{\text{adult}}$ | minimum adult body mass |
| $B_{\text{juvenile}}$ | minimum juvenile body mass |
| $\varepsilon$ | maximum consumption rate |
| $G$ | intrinsic growth rate of resources |
| $n$ | density limiting factor |
| $K_{\text{r}}$ | maximum biomass of resources |
| $c$ | clutch size |
| $x$ | age in general |
| $X$ | age class, i. e. age interval $x$ to $x + 1$ |
| $l_X$ | probability of surviving from birth to beginning of age class $X$ |
| $m_X$ | expected number of offspring for a female in age class $X$ |
| $V_X$ | fecundity for a female in age class $X$ : $l_X m_X$ |
| $\alpha$ | age at maturity, which here means age at first reproduction |
| $T$ | generation time defined as the average age of the mothers of newborn offspring in a population in stable age distribution |
| $LS$ | expected lifespan |

Table 4.1. Furthermore, we will explore the evolutionary consequences of metabolic theory by studying the evolution of minimum adult and juvenile body mass, $B_{\text{adult}}$ and $B_{\text{juvenile}}$, within this model.

### 4.3.1 Influence of the parameter values on life history traits

#### Results from model with density dependent mortality

After 200 years ($200\tau$ in the simulations) the consumer population has reached its equilibrium, i.e., it has obtained a stationary age distribution, and the population size and the total biomass remain approximately constant, due to the density limiting factor $n$. In order to obtain good statistics, the life history traits were evaluated by averaging over two million years, $2 \cdot 10^6 \tau$.

Fig. 4.1 shows an example data set for the fecundity of a female as function of the age class $X$. Fecundity $V_X$ is defined as the product of the expected number of offspring for a female in age class $X$, $m_X$, and the probability of surviving from birth until reaching beginning of age class $X$, $l_X$. In our model only individuals with a body mass above $B_{\text{adult}} + 2B_{\text{juvenile}}$ can reproduce, and it takes in average several years, circa 8 years in this case (Fig. 4.1), to reach the body mass. Therefore, $m_X$ remains zero until the age when an individual for the first time reaches the minimum body mass required to reproduce. This age is called age at maturity in our model.

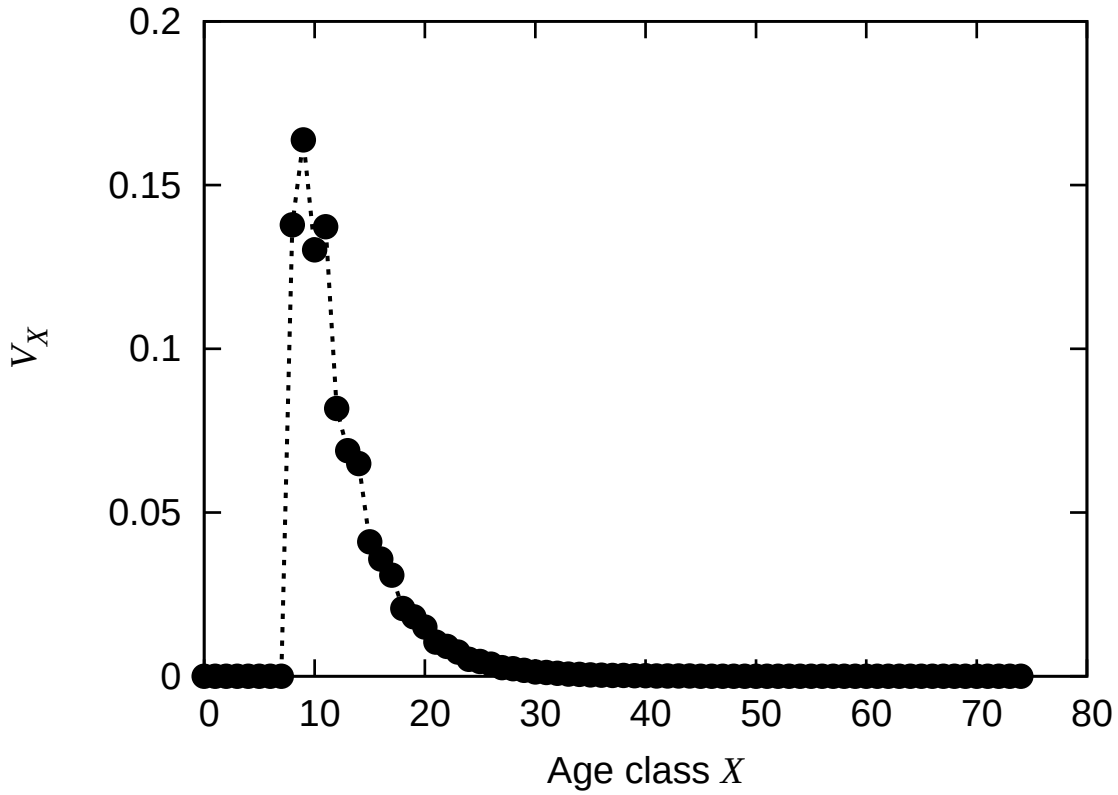



**Figure 4.1.:** Fecundity $V_X$ for a female in age class $X$ (Table 4.1). The parameters applied are $\varepsilon = 15$, $n = 20000$, $G = 1$, $K_r = 40000$, $B_{adult} = 20$.

Reproduction takes place once per year, and the clutch size is determined by the mother's body mass (Eq. (4.6)), which in turn results from resource consumption and metabolism (Eq. (4.2)). Therefore, after maturity $m_X$ is independent of age. Similarly, mortality depends only on body mass and not on age in our simple model. Naturally, $l_X$ decreases monotonously with age. It follows that fecundity is zero until reaching maturity and is thereafter identical to the product of $l_X$ with $m_X$, with the latter parameter being approximately constant. In the following, we will explore in more detail the dependence of $l_X$ on the model parameters.

The survival probability $l_X$ is closely related to mortality, which depends on body mass but not on age (Eq. (4.5)). Since the body mass of an individual remains approximately $B_{\text{adult}}$ after maturity, mortality is approximately constant for adult individuals in an equilibrium population. This means that the survival probability $l_X$ decreases exponentially with age class $X$. This can be seen in Fig. 4.2, where the logarithm of $l_X$ is perfectly linear once maturity has been reached. Since population dynamics are at equilibrium, the body mass of an individual grows within a population of approximately constant total biomass from birth until reaching maturity. Therefore, mortality decreases with age until reaching maturity (Eq. (4.5)), and so does the slope of $\ln l_X$ (Fig. 4.2) for small age classes, i.e., immature individuals.

Fig. 4.2 shows also that adult mortality decreases with decreasing $\varepsilon$, decreasing $G$, decreasing $K_r$, and increasing $n$. The decrease with decreasing $\varepsilon$ or $G$ or $K_r$ is due to the fact that adults that consume less resources produce less offspring, which in turn means less competition from juveniles and therefore a longer life span of the adults. The decrease in adult mortality with increasing $n$ has a similar reason: For larger $n$ the total biomass in the stationary population is larger (Table 4.2), implying that every individual obtains less food and produces fewer offspring. Moreover, mortality is inversely proportional to $n$ according to Eq. (4.5).

Fig. 4.2E shows that the slope of $\ln l_X$ above the age at maturity is smaller for a population of larger adult body mass $B_{\text{adult}}$. This is to be expected since larger individuals have reduced mortality rates. However, before maturity the slope is smaller for a population of individuals of smaller adult body mass (see inset of Fig. 4.2). This means that adults with a smaller body mass are less severe competitors for a juvenile. The reason for this is the larger total biomass of a population with larger $B_{\text{adult}}$ (Table 4.2), which results from the fact that larger individuals have a slower metabolism and can therefore maintain a larger biomass on the same resources.

We also examined the influence of the model variables on other life history traits, such as the age at maturity $\alpha$, the generation time $T$[v], the expected lifespan $LS$, and the expected number of offspring for a female in age class $X$, $m_X$ (Fig. 4.3). We define the age at maturity as the age at which an individual reaches a body mass of at least $B_{\text{adult}} + 2B_{\text{juvenile}}$, when it can give birth to its first offspring. The expected number of offspring, $m_X$, for a female in age class $X$, is zero until reaching maturity, and is independent of age when maturity has been reached. We therefore dropped the index $X$ from $m$ in the figure legend.

We have pointed out above that for larger $K_r$, $\varepsilon$, or $G$, or a smaller $n$, an adult consumes more resources and that the total biomass (Table 4.2) and thus the mortality is larger (Eq. (4.5)). Therefore, the age at maturity, $\alpha$, the generation time, $T$, and the lifespan, $LS$, decrease with

[v] **Generation time** is the average interval between the birth of an individual and the birth of its offspring. - http://www.britannica.com
In the simulation, the mothers' ages of all offspring are summed up and divided by the total number of offspring to determine the mean **generation time** of a population, $T$.

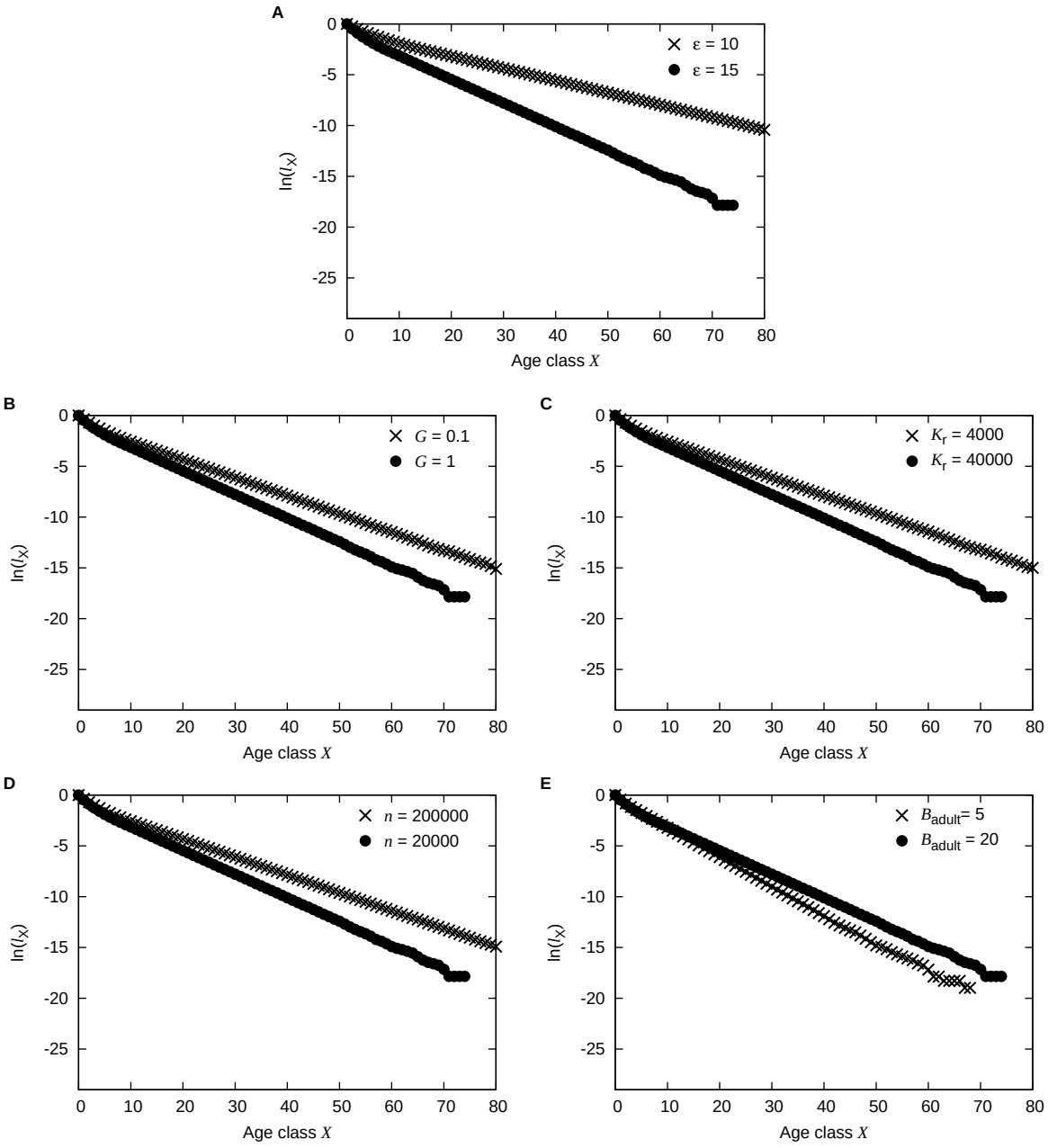



**Figure 4.2.:** Logarithm of the probability of surviving from birth to beginning of age class $X$ in the model with density dependent mortality. The impacts of different variables on the survival probability are shown: (A) maximum consumption rate $\varepsilon$, (B) mass-specific maximum growth rate of the resource $G$, (C) carrying capacity of the resource $K_r$, (D) density limiting factor $n$ and (E) adult body mass $B_{adult}$. Parameters are chosen as in Fig. 4.1 if not labelled.

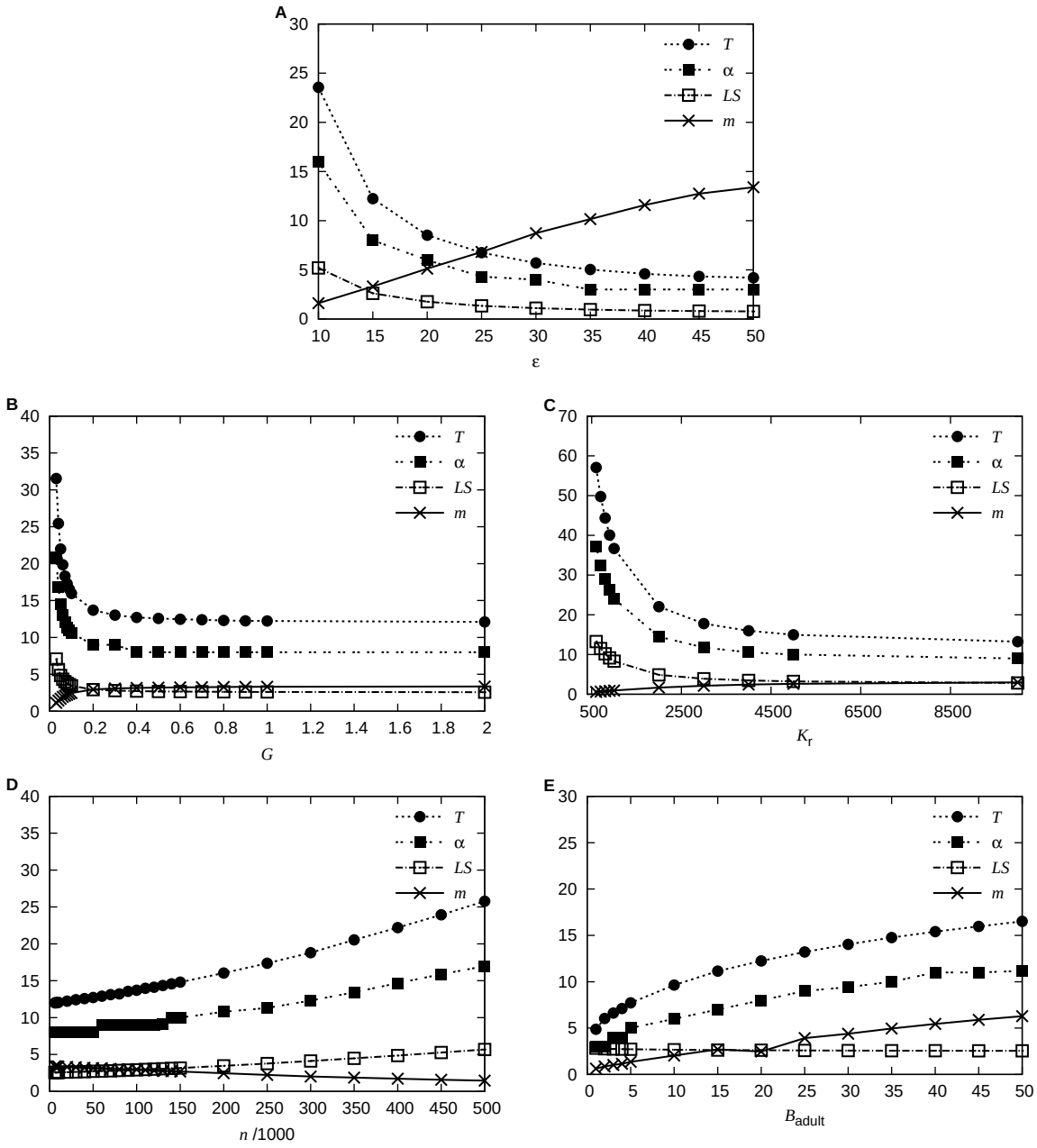



**Figure 4.3.:** Generation time $T$, age at maturity $\alpha$, expected lifespan $LS$, and expected number of offspring for a female per year after maturity $m$ in the model with density dependent mortality. The influence of (A) maximum consumption rate $\varepsilon$, (B) mass-specific maximum growth rate of the resource $G$, (C) carrying capacity of the resource $K_r$, (D) density limiting factor $n$, and (E) adult body mass $B_{adult}$ on $T$, $\alpha$, $LS$, and $m$. Parameters are chosen as in Fig. 4.1 if not varied.

**Table 4.2.:** Influence of single parameter on consumer population and resource biomass in the model with density dependent mortality. The standard parameter set for comparison is as in Fig. 4.1: $\varepsilon = 15$, $G = 1$, $K_\mathrm{r} = 40000$, $n = 20000$, and $B_\mathrm{adult} = 20$. $\downarrow$ indicates that the value is smaller compared with the corresponding one in standard; while $\uparrow$ indicates that the value is larger compared with the standard.

| parameters | Average $\sum_i B_i$ | Average population size | Average $R$ ($R/K_\mathrm{r}$) |
|---|---|---|---|
| Standard | 1018.79 | 124.107 | 38654.8 (0.97) |
| $\varepsilon = 10.$ $\downarrow$ | 514.817 $\downarrow$ | 70.5832 $\downarrow$ | 39544.2 (0.99) $\uparrow$ |
| $G = 0.1$ $\downarrow$ | 770.878 $\downarrow$ | 99.4279 $\downarrow$ | 28162.6 (0.70) $\downarrow$ |
| $K_\mathrm{r} = 4000$ $\downarrow$ | 771.205 $\downarrow$ | 99.4993 $\downarrow$ | 2814.15 (0.70) $\downarrow$ |
| $n = 2 \cdot 10^5$ $\uparrow$ | 7745.44 $\uparrow$ | 998.63 $\uparrow$ | 28100.5 (0.70) $\downarrow$ |
| $B_\mathrm{adult} = 5.$ $\downarrow$ | 947.797 $\downarrow$ | 199.643 $\uparrow$ | 38476.2 (0.96) $\downarrow$ |

increasing $K_r$ or $\varepsilon$ or $G$, and with decreasing $n$. The generation time is of course larger than the age at maturity (Fig. 4.3). The trend of $LS$ follows that of $\alpha$, meaning that populations that mature late live longer. For the same reason, the mean number of offspring per female per year, $m$, increases with increasing $K_r$ or $\varepsilon$ or $G$, and with decreasing $n$. However, since the population is stationary, the total number of offspring that will reach maturity expected per female during her lifetime, is identical to 1.

For sufficiently high resource growth rate, $G$, the curves become constant, because the resource biomass is constrained by its carrying capacity $K_\mathrm{r}$ (Eq. (4.1), Fig. 4.3). Changing the carrying capacity has a similar effect as changing $G$. This can be understood by rewriting Eq. (4.1) as a function of the ratio $\tilde{R} \equiv R/K_\mathrm{r} \in [0, 1]$:

$$\dot{\tilde{R}} = G\left(1 - \tilde{R}\right)\tilde{R} - \frac{1}{K_\mathrm{r}} \sum_{i=\mathrm{consumers}} a\varepsilon B_i^{3/4} \frac{\tilde{R}}{1 + \tilde{R}} \,. \tag{4.8}$$

In this transformed equation, it is obvious that changing $G$ and changing $K_r$ has the same effect on the stationary value of $\tilde{R}$.

The increase of $T$ and $\alpha$ with increasing $B_\mathrm{adult}$ is due to the fact that it takes longer to grow to a larger minimum adult body mass (Fig. 4.4). The increase of $m$ with increasing $B_\mathrm{adult}$ results from the larger food intake of larger individuals, and the shorter lifespan is due to the larger juvenile mortality mentioned earlier.

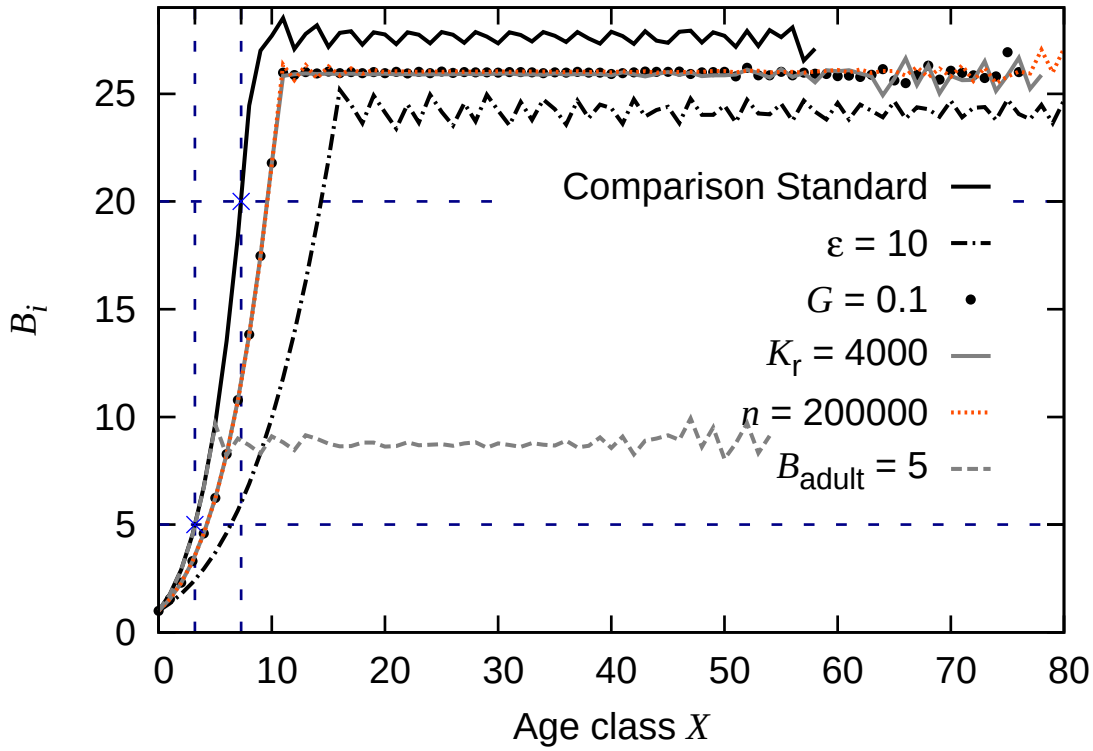



**Figure 4.4.:** Average individual body mass in age class $X$ in the model with density dependent mortality, estimated before possible reproduction. The parameters chosen for the black solid curve are as in Fig. 4.1: $\varepsilon = 15$, $G = 1$, $K_r = 40000$, $n = 20000$, $B_{adult} = 20$. This curve serves as a comparison standard. The gray solid curve is eclipsed by the red dashed curve, except for the tail of the curve where the statistics is suboptimal. The crosses mark the points when an individual in average reaches the minimum adult body mass for the comparison standard and the curve with $B_{adult} = 5$.

## Results from model with density independent mortality

In order to understand which of all the features reported so far are due to the fact that mortality depends on density, we also investigated the case where mortality is independent of density, i.e.,

$$\chi_i^{(\text{density independent})} = \mu B_i^{-0.25} \tag{4.9}$$

with a new parameter $\mu$ that plays a similar role as $1/n$. One can also imagine mortality to depend on the sum $\sum_i \xi B_i \propto \sum_i B_i^{0.75}$ instead of the sum $\sum_i B_i$ in Eq. (4.5), a situation that is intermediate between these two cases.

When mortality is density independent, the slope of the age specific survival probability $l_X$ does not depend on $G$, $\varepsilon$, and $K_\mathrm{r}$ (Fig. 4.5), since the mortality is solely determined by the individual's body mass $B_i$ (Eq. (4.9)), which is approximately $B_\mathrm{adult}$ after maturity. The slope, determined by mortality, increases with increasing $\mu$ and decreasing $B_\mathrm{adult}$, since mortality is proportional to $\mu$ and inversely proportional to $B_i (\sim B_\mathrm{adult}$ after maturity). When $\mu$ or $B_\mathrm{adult}$ are changed, the trends of $T$, $\alpha$, $LS$, and $m$ are the same as in the density dependent case for changing $1/n$ or $B_\mathrm{adult}$ (Fig. 4.3). The mechanisms causing these trends remain the same. Since survival probability is independent of $G$, $K_\mathrm{r}$ and $\varepsilon$, the age structure of the population is also independent of these parameters, as is the amount of resources consumed per individual. Therefore, the generation time, life span, age at maturity and mean number of offspring per female per year do not depend on these parameters either (Fig. 4.6). The only change that occurs when these parameters are increased is an increase in the total population size (Table 4.3). The fraction of available resource at equilibrium, $R/K_\mathrm{r}$, is kept at the same level with increasing $G$ and $K_\mathrm{r}$, while this fraction significantly decreases with increasing $\varepsilon$ (Table 4.3). For this reason, the increase in population size with increasing $\varepsilon$ lasts only up to a certain value, then the population size decreases as $\varepsilon$ increases further.

However, the change of the equilibrium resource biomass $R$ with $B_\mathrm{adult}$ is different in the two cases. When mortality is density dependent, $R$ increases with increasing $B_\mathrm{adult}$ (Table 4.2), while it decreases in the density independent case (Table 4.3). In both cases, the total biomass increases with increasing $B_\mathrm{adult}$ (Table 4.2 and Table 4.3). However, a density dependent mortality counteracts the increase of the total biomass by killing more individuals when total biomass becomes larger. The result is that the increase in total biomass is weaker than $B_\mathrm{adult}^{0.25}$ (Eq. (4.5)), which would be the increase required to obtain the same level of resource exploitation as in the case with density independent mortality.

Figure 4.7 shows the average body mass of individuals in age class $X$. The average growth rate of an individual's body mass remains the same as the value of the three parameters, $\varepsilon$, $G$ and $K_\mathrm{r}$, are changed. As stated above, the amount of resources consumed per individual is independent of $\varepsilon$, $G$ and $K_\mathrm{r}$. The explanation is straightforward in cases of $G$ and $K_\mathrm{r}$, since the population size linearly increases with increasing $G$ and $K_\mathrm{r}$ (Table 4.3). When the maximum consumption rate $\varepsilon$ increases, however, a higher growth rate of an individual's body mass can be expected. Yet the effect of increasing $\varepsilon$ is compensated by the increasing population size and the decreasing biomass of resources (Table 4.3). On average, an individual grows faster when the mortality becomes higher, i.e., the amount of resources consumed per individual is larger. As shown in Table 4.3, the population size decreases with increasing mortality, while the

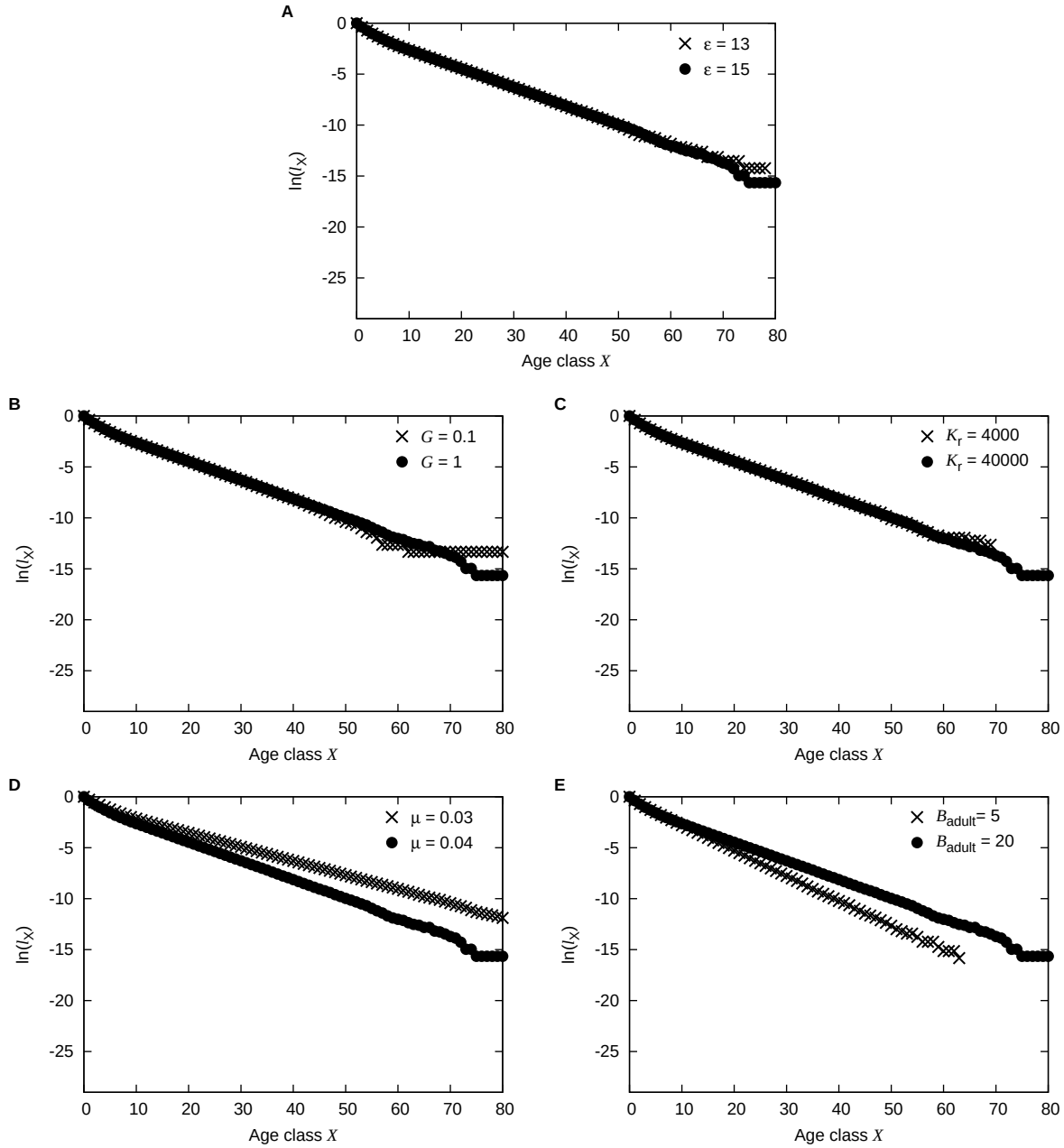



**Figure 4.5.:** Logarithm of the probability of surviving from birth to beginning of age class $X$, in the model with density independent mortality. The impacts of different variables on the survival probability are shown: (A) maximum consumption rate $\varepsilon$, (B) mass-specific maximum growth rate of the resource $G$, (C) carrying capacity of the resource $K_\mathrm{r}$, (D) the new parameter adjusting mortality $\mu$ (playing a similar role as $1/n$ in case of density dependent mortality) and (E) adult body mass $B_\mathrm{adult}$. Parameters are chosen as in Fig. 4.1 if not labelled: $\varepsilon = 15$, $G = 1$, $K_\mathrm{r} = 40000$, $B_\mathrm{adult} = 20$, and the new parameter $\mu = 0.04$.

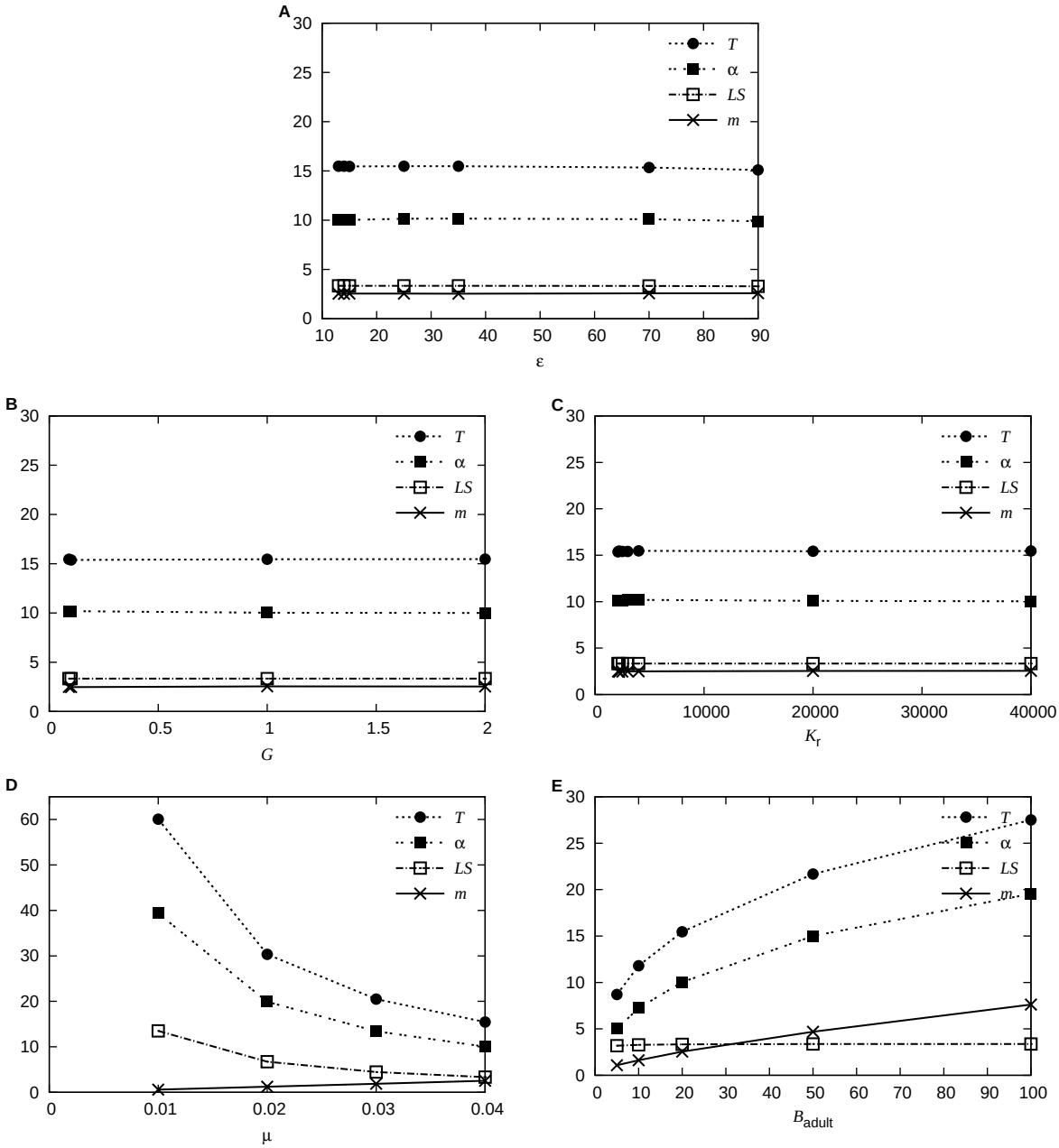



**Figure 4.6.:** Generation time $T$, age at maturity $\alpha$, expected lifespan $LS$ and expected number of offspring for a female per year after maturity $m$, in the model with density independent mortality. The influence of (A) maximum consumption rate $\varepsilon$, (B) mass-specific maximum growth rate of the resource $G$, (C) carrying capacity of the resource $K_r$, (D) the new parameter adjusting mortality $\mu$ (playing a similar role as $n$ in case of density dependent mortality) and (E) adult body mass $B_{adult}$ on $T$, $\alpha$, $LS$ and $m$. Parameters are chosen as in Fig. 4.1 if not varied: $\varepsilon = 15$, $G = 1$, $K_r = 40000$, $B_{adult} = 20$, and the new parameter $\mu = 0.04$.

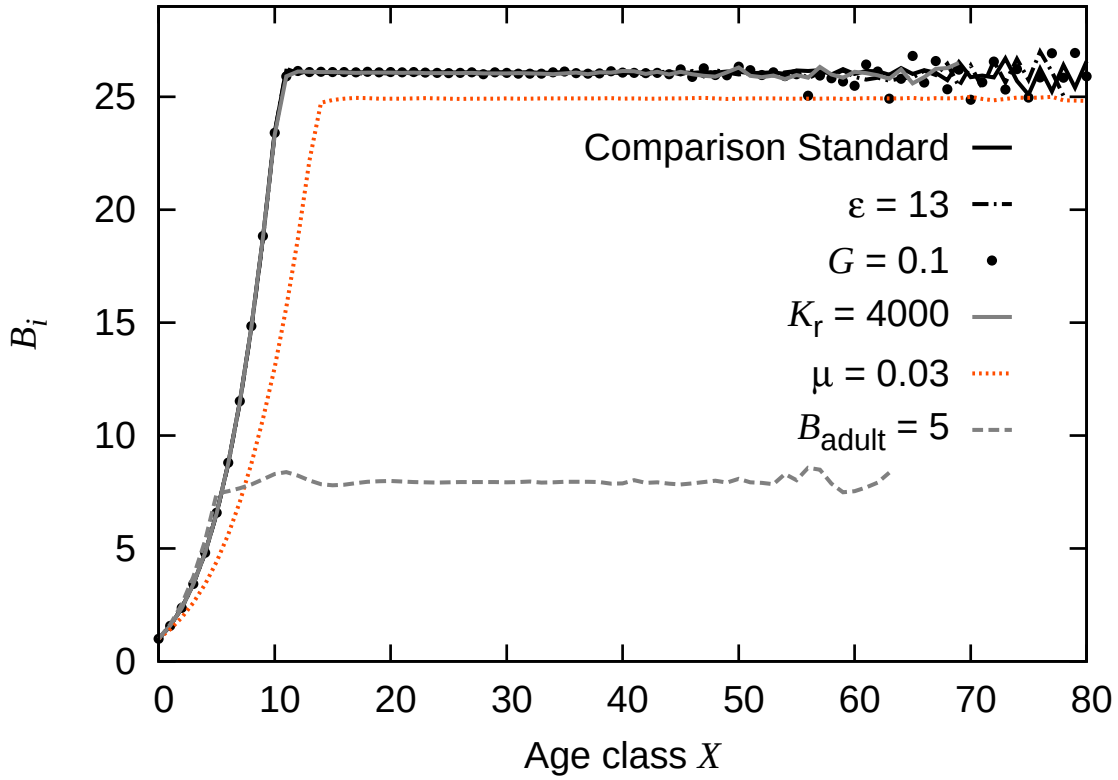



**Figure 4.7.:** Average individual body mass in age class $X$ in the model with density independent mortality, estimated before possible reproduction. The parameters chosen for the black solid curve are as in Fig. 4.1: $\varepsilon = 15$, $G = 1$, $K_r = 40000$, $B_{adult} = 20$, and the new parameter adjusting the mortality $\mu = 0.04$. The black solid curve serves as a comparison standard. This curve is eclipsed by the curves labeled with varied values of $\varepsilon$, $G$ and $K_r$, except for the tail of the curve where the statistics is suboptimal.

**Table 4.3.:** Influence of single parameter on consumer population and resource biomass in the model with density independent mortality. The standard parameter set for comparison is: $\varepsilon = 15$, $G = 1$, $K_r = 40000$, $\mu = 0.04$, and $B_{adult} = 20$. $\downarrow$ indicates that the value is smaller compared with the corresponding one in standard; while $\uparrow$ indicates that the value is larger compared with the standard, and $\circ$ indicates that the value is hardly changed.

| parameters | Average $\sum_i B_i$ | Average population size | Average $R$ ($R/K_r$) |
|---|---|---|---|
| Standard | 7152.95 | 919.907 | 29179.2 (0.73) |
| $\varepsilon = 13. \downarrow$ | 1718.24 $\downarrow$ | 221.272 $\downarrow$ | 38015.3 (0.95) $\uparrow$ |
| $G = 0.1 \downarrow$ | 700.48 $\downarrow$ | 90.0226 $\downarrow$ | 29387.5 (0.73) $\circ$ |
| $K_r = 4000 \downarrow$ | 702.899 $\downarrow$ | 90.3101 $\downarrow$ | 2934.55 (0.73) $\downarrow$ ($\circ$) |
| $\mu = 0.03 \downarrow$ | 10470.6 $\uparrow$ | 1409.75 $\uparrow$ | 22298.6 (0.56) $\downarrow$ |
| $B_{adult} = 5. \downarrow$ | 4554.83 $\downarrow$ | 1039.62 $\uparrow$ | 31850.7 (0.80) $\uparrow$ |

average resource biomass at equilibrium increases. With increasing $B_{adult}$, both population size and the average resource biomass decreases (Table 4.3). Therefore, the amount of resources consumed per individual remains the same. Yet a marginal decrease in the body mass growth rate is observable from birth until maturity, as $B_{adult}$ increases (Fig. 4.7). The reason is the severe competition with adults for resources as the minimum adult body mass $B_{adult}$ becomes significant larger than the body mass of a juvenile.

### 4.3.2 Evolution of body mass

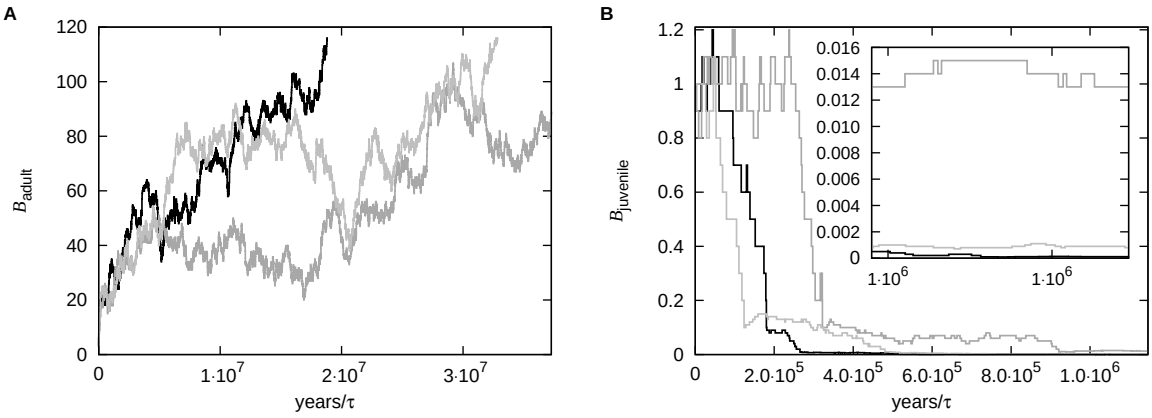



**Figure 4.8.:** Evolution of (A) adult body mass $B_{adult}$ and (B) juvenile body mass $B_{juvenile}$ in the model with density dependent mortality. Parameters are chosen as in Fig. 4.1 if not varied. (Black, dark grey and grey curves are results from three independent simulations with different series of random numbers.)

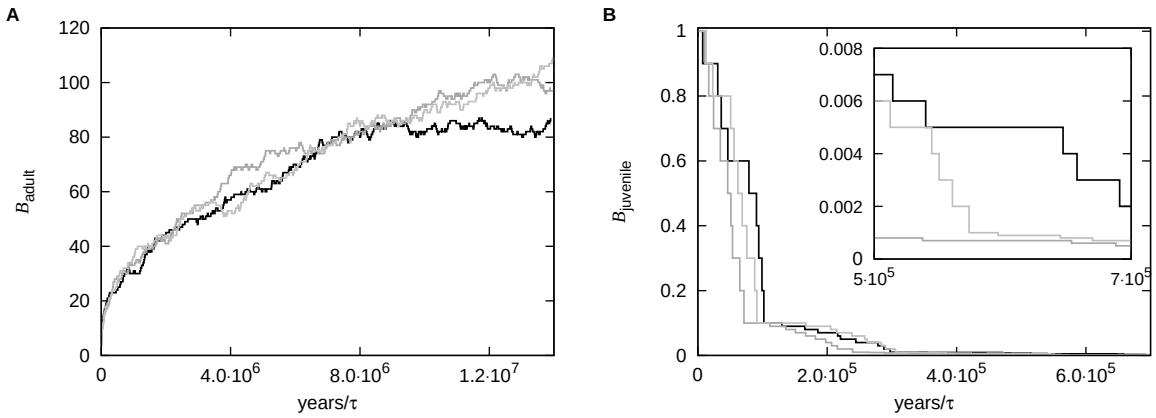



**Figure 4.9.:** Evolution of (A) adult body mass $B_{\text{adult}}$ and (B) juvenile body mass $B_{\text{juvenile}}$ in the model with density independent mortality. Parameters are chosen as in Fig. 4.1 if not varied, and $\mu = 0.03$. (Black, dark grey and grey curves are results from three independent simulations with different series of random numbers.)

All investigations reported so far were performed with a fixed adult body mass $B_{\text{adult}}$ and a fixed minimum juvenile body mass $B_{\text{juvenile}}$. However, these two values are the result of evolutionary processes, and on the long run those body masses will dominate that are the best "strategies" for dividing resources between growth and offspring production. We performed separate computer simulations for the evolution of the minimum adult body mass $B_{\text{adult}}$ and of the minimum juvenile body mass $B_{\text{juvenile}}$. After 200 years, we assigned to half of the offspring born in this year a modified adult or juvenile body mass $B_{\text{mutant}} = B_{\text{original}} \pm \Delta$ ("+" or "−" is randomly chosen, but the chosen one is then applied for all mutants). In computer simulations for the evolution of adult body mass we set $\Delta = 1$, and in computer simulations for the evolution of the juvenile body mass $\Delta = 0.1$ for $B_{\text{original}} > 0.1$ and $\Delta = 0.01$ for $0.01 < B_{\text{original}} \leq 0.1$ etc.. We then let the simulations run until one of the two strategies present in the population had driven the other to extinction. Then we waited for another 200 years before introducing another mutant by modifying again the adult or minimum juvenile body mass of half of the newborn offspring.

Fig. 4.8 shows three independent simulation runs for the evolution of adult body mass and for the evolution of juvenile body mass in case of density dependent mortality. The evolution of adult body mass looks like a random walk with a bias towards increasing $B_{\text{adult}}$. This means that an individual with a larger adult body mass has on average more children during its lifetime than an individual with a smaller body mass. This follows indeed from the allometric scaling of the terms contributing to population dynamics: An individual that matures 1 year later than the other members in its age class, starts producing children one year later. But then it has on average more children per year and a lower mortality than other individuals of the same age, obtaining in total more children during its life time. This conclusion holds of course only as long as there are no disadvantages to larger body mass. Here, however, we can only expect an increase of $B_{\text{adult}}$, since our model only includes the advantage of having a slower metabolism. Moreover, the evolution towards larger body mass depends crucially on the fact that mortality decreases as $B_{\text{adult}}^{-0.25}$ with increasing body mass (Eq. (4.5)), which means that mortality scales the same way as resource consumption and metabolism. Therefore the evolution of adult body

mass in case of density independent mortality (Eq. (4.9)) also has the trends towards larger body mass (Fig. 4.9). If mortality decreased slower with increasing body mass, the biomass loss due to mortality would eventually become larger than the biomass gain due to resource consumption. In this case, the evolutionary increase of $B_{\text{adult}}$ would eventually stop.

The evolution of juvenile body mass shows the opposite trend (Fig. 4.8 and 4.9). This means that it is always better to produce smaller offspring in our model. In order to understand this, let us compare the production of an offspring of body mass $B_{\text{juvenile}}$ with the production of two offspring of size $B_{\text{juvenile}}/2$. If each of the two small offspring have a chance larger than 1/2 to survive until they reach the body mass $B_{\text{juvenile}}$, then an adult that produces the smaller offspring will have more surviving children during its lifetime than an adult that produces the larger offspring. Indeed, the total biomass of all individuals that were born at the same time increases with time, until maturity is reached. Consequently, after the time required for an offspring born with body mass $B_{\text{juvenile}}/2$ to grow to the body mass $B_{\text{juvenile}}$, the expected total biomass of the two offspring is larger than $B_{\text{juvenile}}$. This means that the chance that a small offspring survives until reaching $B_{\text{juvenile}}$ is larger than 1/2. All this is a result of the mortality scaling in the same way as resource consumption and metabolism. Because all three determinants of growth scale in the same way with body mass, the rate of change of the total biomass of all individuals that were born at the same time is a constant. This constant cannot be negative, since the population would then die out. Therefore, it must be positive, with the result that it always pays off to produce smaller offspring. If mortality increased stronger with decreasing body mass, there would be a minimum offspring body mass.

## 4.4 Discussion

We have investigated the life history traits of a population feeding on resources which regrow by using a model that explicitly considers the dynamics of both the consumers and the resources. The model takes into account the allometric scaling of resource consumption, metabolism and mortality with the body mass of the consumer. Since no other factors are taken into account, this is a minimal model that investigates in the simplest possible form the effect of allometric scaling on life history features. These life history features are evaluated in a stationary population. Despite the simplicity of the model, several life history characteristics known from natural systems emerge correctly from the model, for instance the correlation between age at maturity and longevity (Migliano *et al.*, 2007; Pettay *et al.*, 2005), the observation that resource scarceness or slow resource intake leads to a longer lifetime (Kirkwood and Shanley, 2005; McCay *et al.*, 1935; Wolf, 2006), or the finding that larger clutch size is correlated with larger juvenile mortality (Martin, 1987). The reason behind these trends in our model is the following: Populations that consume less resources have a slower growth and a smaller rate of offspring production. Due to the slower growth, maturity sets in later. Due to the smaller number of offspring, there is a decreased density dependent mortality and therefore a larger life expectancy. In our model, these correlations occur in stationary homogeneous populations, where all individuals of the same body mass are equivalent. When an individual with restricted resource intake is placed in a well fed and fast growing population in our model, its mortality is the same as that of the other individuals of the same body mass, because mortality is determined by population density and body mass alone. In contrast, in laboratory populations individuals

that obtain less food live longer than well-fed individuals, due to the physiological changes occurring in these individuals. We suggest that this response to food shortage may ultimately be shaped by evolutionary history, since earlier ageing does not confer a substantial disadvantage in stationary well-fed populations, but in resource restricted populations. Therefore, a mutant aging earlier might establish in well-fed populations but not in populations restricted in resource supply during evolution.

When adult body mass is allowed to evolve, it increases without limits in this simple model - until the population crashes because the number of individuals has become so small that random fluctuations can cause its extinction. This finding demonstrates that Cope's rule can result from allometric scaling alone, without taking into account other advantages of large body mass. An important condition for the evolution towards larger body mass is that the population is stationary. If the population was growing exponentially, individuals that have a smaller adult body mass and thus produce offspring earlier could multiply faster. Another important condition for the evolution towards larger body mass is that there are no causes of mortality that deviate from allometric scaling. In order to produce pygmies, the model would need to include a mortality that is for instance independent of body mass. Another possible cause behind smaller adults may be recurring catastrophic events that kill a large portion of the population. During the subsequent population expansion, smaller adult body masses would confer an advantage due to the earlier onset of reproduction.

We also found that the offspring body mass evolves towards smaller and smaller size in the allometric model. In our model, the offspring body mass is the body mass that the offspring reached when parents stopped nourishing them. Furthermore, we have assumed that the investment into offspring is twice the body mass of the offspring. The result of our model suggests that a minimum offspring body mass can not be explained based on allometric scaling alone. The evolution of offspring body mass can therefore only be understood by taking into account the many factors that affect infant mortality and the parental investment required to produce offspring of a given body mass. An important determinant of juvenile mortality is predation. The effect of predation on juveniles does not scale with body mass, smaller prey are consumed by a larger number of predators and with increasing body mass prey moves towards size refuges from predation of an increasing number of predators. This is most pronounced in aquatic systems where prey swallowing is limited by the gape width of fish predators (Christensen, 1996; Persson *et al.*, 1996). In fact, there is evidence that e.g. predation on fish eggs of different mass follows a hump shape curve (Paradis *et al.*, 1996). On the other hand, trade-offs concerning predation success also limit adult body mass. The evolution towards lower body mass of offspring in our model therefore lacks realism. However, our goal is to explore the evolution of life history characteristics based on the metabolic theory, i.e., not only thereby uncover the predictive power but also the limits of the metabolic theory. Recently, it has been shown that foraging theory (Brose *et al.*, 2006, 2008) that considers the relation between prey capture success and predator body mass needs to be incorporated to understand predator - prey body mass ratios . Rather than by a power law function, as predicted by the metabolic theory (Brown *et al.*, 2004), energy flux in predator - prey interactions peaks at intermediate body mass of the predator as the escape efficiency of prey increases beyond a certain threshold of predator body mass (Vucic-Pestic *et al.*, 2010). The evolution towards higher body mass of adult body mass in our model apparently lacks realism as it is based solely on metabolic theory and ignores foraging theory.

Again, it our intention is to explore the strengths and limits of metabolic theory in predicting life history characteristics. In the evolution of offspring body mass, limitations of the theory are most obvious and the integration of foraging theory considering predator - prey body mass ratios is in general needed.

In this chapter we presented a life history model that solely takes into account resource use and metabolic scaling. Despite its simplicity and abstraction of nature, this model reproduces fundamental life history characteristics of species, such as number of offspring and longevity, which are in large consistent with nature. This was achieved by combining metabolic theory with consumer resource dynamics in stationary populations. The results reflect that resources not only play a fundamental role in ecological processes, i.e. at short time scales, but also for shaping life histories, i.e. at evolutionary time scales. As the ingredients of the model are very fundamental and apply to any organisms consuming resources, consumer - resource dynamics combined with metabolic theory provide a null model for evaluating the role of other factors, such as predation, environmental stochasticity and spatial or temporal resource distribution, and for the evolution of life history characteristics in future studies.

# 5 The ecological advantage of sexual reproduction in multicellular long-lived organisms

We present a model for the advantage of sexual reproduction in multicellular long-lived species in a world of structured resources in short supply. The model combines features of the Tangled Bank and the Red Queen hypotheses of sexual reproduction, and is of broad applicability. The model is ecologically explicit with the dynamics of resources and consumers being modelled by differential equations. The life history of consumers is shaped by body-mass dependent rates as implemented in the metabolic theory of ecology. We find that over a broad range of parameters sexual reproduction wins despite the twofold cost of producing males, due to the advantage of producing offspring that can exploit underutilized resources. The advantage is largest when maturation and production of offspring set in before the resources of the parents become depleted, but not too early, due to the cost of producing males. The model thus leads to the dominance of sexual reproduction in multicellular animals that live in complex environments, with resource availability being the most important factor affecting survival and reproduction.

## 5.1 Introduction

While traditional population genetics models of evolution assign fitness values directly to genotypes, models based on ecological interactions calculate the survival and reproduction of species by considering their interactions with resources and other species. This approach also has been adopted in models on the evolution and maintenance of sex. The disadvantage of sex is that females have to produce males which do not themselves produce offspring, and thereby encounter a twofold disadvantage in the number of offspring produced per generation (Maynard Smith, 1978; Williams, 1975). Yet, in spite of this twofold cost, most species are sexual. Among genetic models of sex, Muller's ratchet (Muller, 1932, 1964) has been the most prominent (Felsenstein, 1974; Manning, 1976). It assumes that the advantage of sex lies in eliminating deleterious mutations, thereby preventing mutational meltdown. However, this advantage is only experienced in the long term, and models drawing on long-term advantages have been assumed to be insufficient to explain the predominance of sexual reproduction (Bell, 1982; Maynard Smith, 1978; Williams, 1975). Rather, there must be short-term advantages balancing the large costs associated with the production of males.

Population genetics models that yield short-term advantages of sexual reproduction are lottery models (Williams, 1975), which assume that the environment is unpredictable and therefore the fitness of offspring genotypes varies at random and is independent of the fitness of parent genotypes in the previous generations. However, as pointed out by Bell (1982), lottery models are in conflict with the observation that harsh and unstable environments favor asexual rather than sexual reproduction. The two most important ecological hypotheses for the maintenance of sexual reproduction have been the Red Queen hypothesis and the Tangled Bank hypothesis, both of which stress the importance of interactions with other species. The Red Queen hypothesis is most vividly illustrated by the arms race between host and parasite (Hamilton, 1980; Jaenike,

1978) or predator and prey, but it is also applied more generally to the temporal change in the interaction between a species and its environment (Bell, 1987; Salathe *et al.*, 2008). In contrast, the Tangled Bank is based on the spatial heterogeneity of the environment (Bell, 1982; Maynard Smith, 1978), emphasizing that genetically diverse offspring can exploit a broader spectrum of resources. Currently, the Red Queen hypothesis has become the most popular explanation for the short-term advantage of sexual reproduction (Lively and Dybdahl, 2000; Lively, 2009), although it is doubted that Red Queen processes are sufficient for explaining the dominance of sexual reproduction (Salathe *et al.*, 2008; S. West *et al.*, 1999).

Doebeli (1996) argued that a theory that combines Red Queen and Tangled Bank processes is the most promising (Chapter 1). Among others, such a theory enables offspring with a different genotype than their parents to exploit resources that have not been depleted by their parents. This represents a negative feedback in resource use of parents to that of offspring, resulting in an ongoing change with time in the usage of a broad set of resources in heterogeneous space by consumers with continuously changing genotypes (Chapter 2). As shown in Chapter 2 and 3), the structured resource model combines features of both the Tangled Bank and the Red Queen theory. The model successfully predicts the predominance of sexual reproduction over a large parameter range when resource diversity is high, resources regrow slowly and are in limited supply. When a spatial dimension is included (Chapter 2 and 3), the model also successfully predicts the geographic distribution of sexual and parthenogenetic reproduction, i.e., the dominance of sexual reproduction in favorable environments and the dominance of asexual reproduction in harsh environments, a phenomenon termed geographic parthenogenesis (Vandel, 1928).

Before this work, no model exists targeting the maintenance of sex of multicellular long-lived species that explicitly includes the dynamics of the resources used by such species. Such a model requires the implementation of life-history traits such as growth until maturity and size- or age-dependent mortality. A life-history model that is based on metabolic theory (Brown *et al.*, 2004) is presented in the previous chapter. Combining consumer-resource dynamics with metabolic theory, this model constitutes the basis for including resource diversity in space and time and the associated fitness benefits of sexual vs. asexual reproduction. In this chapter, we present a model that combines life history theory with features of the structured resource model of sex (Scheu and Drossel, 2007). This model provides a general theory on the maintenance of sexual reproduction in multicellular long-lived species, such as virtually all metazoan animals[i]. The model combines Tangled Bank and Red Queen processes by modelling the dynamics of consumers and structured resources in short supply.

## 5.2 Structured resource model for long-lived organisms

We consider a patch that contains several different resources and several consumer individuals. In order to take the extension of space into account, we later also consider several such patches that are connected by migration of the consumers.

The genetic algorithms are the same as in Chapter 2. A patch contains $L \times L$ different resources. Resources are numbered by $j = 1, \ldots, L^2$, with the niche coordinates of resource $j$

[i] **Metazoan animals** in Glossary.

being $(x_j, y_j) \in [1, L] \times [1, L]$. Consumer genotypes are labelled in the same way. A consumer with the genotype $i$ is best adapted to resource $j = i$, but can also feed on resources with neighboring niche values, as long as the $x$ and $y$ values of resource and consumer differ by no more than 2. (The cut-off is for computational convenience, and it is also legitimate as the attractiveness of other resources for the consumer is negligible (Eq. (5.4).)

The population dynamics are similar as described in the previous chapter. Resources continuously grow according to the logistic equation with a maximum growth rate $G$ and carrying capacity $K_\mathrm{r}$, and lose biomass due to being consumed, which leads to the equations

$$\dot{R}_j = G\left(1 - \frac{R_j}{K_\mathrm{r}}\right)R_j - \sum_{i=\text{consumers}} \xi_i \varepsilon B_i F_{ij}\,, \tag{5.1}$$

$B_i$ is the body mass of consumer $i$, and the sum is taken over all consumer individuals. As in the previous chapter the life cycle of consumer individuals is tailored to iteroparous species, i.e., multicellular long-lived organisms that reproduce more than once per life time, which is typical for large metazoan animals, in particular vertebrates such as lizards (Ballinger, 1977) and deer (Gaillard and Yoccoz, 2003). After birth the body mass $B_i$ of an individual $i$ increases from the initial value $B_\text{juvenile} = 1$ due to resource consumption that results in somatic growth, and the body mass decreases due to respiration according to the equation

$$\dot{B}_i = -\xi_i B_i + \lambda \xi_i \varepsilon B_i \sum_{j=\text{resources}} F_{ij}\,, \tag{5.2}$$

where $\xi_i$ is described by Eq. 4.4, i.e., the decline in body mass due to respiration is proportional to $B_i^{3/4}$. The allometric constant $a$ is 0.314 (Rall *et al.*, 2008) as in the previous chapter . Larger individuals need less energy per body mass for metabolism. When the body mass gained by resource consumption does not outweigh the cost of metabolism, the individual loses weight. Once the body mass drops below the offspring weight $B_\text{juvenile}$, the individual is considered dead and removed from the system.

The ecological efficiency $\lambda$ is chosen to be $0.4$ (Turner, 1970), and the maximum consumption rate $\varepsilon$ of the consumers relative to their metabolic rate is a parameter of the model. The function $F_{ij}$ was chosen to be a Holling type II functional response (Holling, 1959),

$$F_{ij} = \frac{\alpha_{ij} R_j / K_\mathrm{r}}{1 + \sum_{l=\text{resources}} \alpha_{il} R_l / K_\mathrm{r}}\,, \tag{5.3}$$

where

$$\alpha_{ij} = \Omega e^{-(x_j - x_i)^2 - (y_j - y_i)^2} \tag{5.4}$$

measures the attractiveness of resource $j$ for consumer $i$. $\Omega$ is chosen in a way that $\sum_j \alpha_{ij} = 1$ for all $i$. As mentioned above, $\alpha_{ij}$ is set to zero when $(x_j - x_i)^2 + (y_j - y_i)^2 > 8$.

Mortality depends on body mass and density. Since an individual dies as a whole not partially, mortality is implemented as a probability for occasional death in our individual-based model. A year has the duration $\tau = 1$. At the end of every time interval $\Delta t = 0.1$, each individual

dies with a probability $p \in [0, 1]$ (Eq. 4.5) depending on its body mass and the total consumer biomass. Larger individuals have a smaller probability of dying. Mortality is scaled with body mass in the same way as metabolism, in agreement with empirical data (Brown *et al.*, 2004). Mortality is high in population with large total consumer biomass. The parameter $n$ (Eq. 4.5) is related to the maximum biomass imposed by the limited space of the system. Dead individuals are removed from the system.

Once per year, reproduction takes place, just before the first death events of that year. An individual, sexual or asexual, is considered mature once it has reached the minimum adult body mass $B_{\text{adult}}$. An asexual female with a body mass $B_{\text{mother,prev}}$ larger than $B_{\text{adult}}$ by at least twice the offspring weight $B_{\text{juvenile}}$ produces $c$ offspring (Eq. 4.6) rounded to an integer) with body mass $B_{\text{juvenile}} = 1$. Taking into account parental care such as nursing and feeding, we assume the investment of a female to be twice $B_{\text{juvenile}}$ for each offspring. Offspring body mass $B_{\text{juvenile}}$ is the minimum juvenile body mass after parents have stopped investing into their offspring, i.e., when juveniles begin to independently feed on resources. The genotype, $(x_i, y_i)$, of an asexual offspring is identical with that of its mother.

For a mature sexual female to reproduce, there must be mature males in the same patch. Sexual females mate with a randomly chosen partner, with the probability of a male to be chosen being proportional to its body mass, assuming that female mate choice is largely based on male body size (Andersson, 1994; Clutton-Brock and McAuliffe, 2009). The number of offspring produced by a sexual female and its decline in body mass due to reproduction are calculated the same way as for asexual females. The genotype of a sexual offspring is chosen randomly from a Gaussian distribution around the midparent value of each of the two genotype trait values, rounded to the nearest integer that still lies within the allowed range $[1, L]$. The variance of the Gaussian distribution is $V_{\text{g}} = 2.5^2$ in both dimensions. With a small probability $u = 0.001$ a sexual offspring becomes asexual, based on the fact that asexual lineages can arise in sexual populations, in agreement with the 'frozen niche variation hypothesis' of Vrijenhoek (1979). The remaining sexual offspring have a probability of 1/2 to be female or male. After reproduction, the body mass of males decrease to $B_{\text{adult}} + 2 \cdot B_{\text{juvenile}}$ if they are larger than this value. This prevents males from becoming ever larger, and is justified by the cost of competing for mates (Andersson, 1994). Note that we have not included investment of the father into rearing offspring, which would result in a larger offspring body mass or a smaller mortality of sexual offspring compared to asexual offspring (Clutton-Brock, 1991). By omitting this benefit for the sexual offspring, we implement the full twofold cost of having males in the sexual populations. Only if this cost is more than compensated for by the advantage of being able to use additional resources, the sexual populations do have a chance to win.

## 5.3 Results

### 5.3.1 Simulation setups

We perform computer simulations of the model in order to determine the dominant mode of reproduction. The model is initiated with a maximum resource biomass $R_j = K_{\text{r}} = 100$ in each niche, and with 20 asexual individuals and 20 sexual individuals with randomly chosen

genotypes. Half of the sexual individuals are male and half are female (as visualized in Fig. 5.3 of section 5.5).

We run the processes of growth, feeding, death, and reproduction for 1000 years before evaluating the proportion of sexual individuals. The simulations are performed for different values of the three ecological parameters, resource diversity $L$, intrinsic resource growth rate $G$ ($K_r$ has an effect similar to that of $G$), and the population limiting factor $n$, which is a measure of the extent to which population density is regulated by factors other than resource availability. The influence of the maximum consumption rate $\varepsilon$ and the minimum adult body mass $B_{\text{adult}}$ on the dominance of sexual reproduction are also investigated. All results are averaged over 1000 simulations.

### 5.3.2 Advantage of sexual reproduction as a function of the parameters

Figure 5.1 shows the average percentage of sexual females among all females in each patch after $1000\tau$, which corresponds to between 7 and 146 generations, depending on the parameters (see Fig. 5.5 in section 5.5 for more details). The typical generation time is $12\tau$ for the standard parameter set of $B_{\text{adult}} = 15$, $\varepsilon = 20$, $L = 20$, $G = 0.1$ and $n = 20000$. In general, the mean generation time of sexual females is shorter than that of asexual females (Fig. 5.5 in section 5.5). Since sexual offspring can exploit resources different from those of their parents and siblings, a sexual individual obtains on average more resources than an asexual individual and grows faster. On average, it takes less than $700\tau$ either for the sexual population or for the asexual population to drive the other to extinction. Usually, the sexual population cannot win during the first few generations, when resources are still abundant and asexuals have higher productivity. Even when none of the two reproduction modes has won after $1000\tau$, this time period is sufficient to obtain an equilibrium composition of sexual and asexual individuals. Actually, $600\tau$ is long enough, a comparison of results after $600\tau$ and $1000\tau$ showed no difference.

Figure 5.1A shows the average percentage of sexual females after $1000\tau$ as a function of the maximum consumption rate $\varepsilon$. When the consumption rate is small, resource exploitation is low, and there is no advantage to sexual reproduction, rather, the disadvantage of producing males prevails. The larger $\varepsilon$, the heavier is the exploitation of resources and the larger is the advantage of sexual reproduction, as manifested by the close to 100 percent success of the sexual lineages. The ability of sexual offspring to exploit resources in other underutilized niches is of great advantage.

Similar mechanisms underlie the results shown in Figure 5.1B and Figure 5.1C. Slow growth of resources (i.e., small values of $G$) or low mortality (i.e., large values of $n$) results in heavy exploitation of resources, and sexual reproduction dominates since sexual offspring can exploit unused resources, outweighing again the cost of producing males. In the opposite situation, when fast resource growth or high mortality prevent strong resource exploitation, there is no advantage of being sexual, then asexuals win.

In contrast to the original model for short-lived species (Scheu and Drossel, 2007), sexual reproduction still dominates for values of $n$ that are so large that a considerable fraction of the niches are occupied in the patch. This is because asexual individuals coexist with their offspring in the same niche, but if the resources in this niche do not regrow fast enough, the niche cannot sustain the parent individual and its offspring. Therefore, they are soon outnumbered by sexual

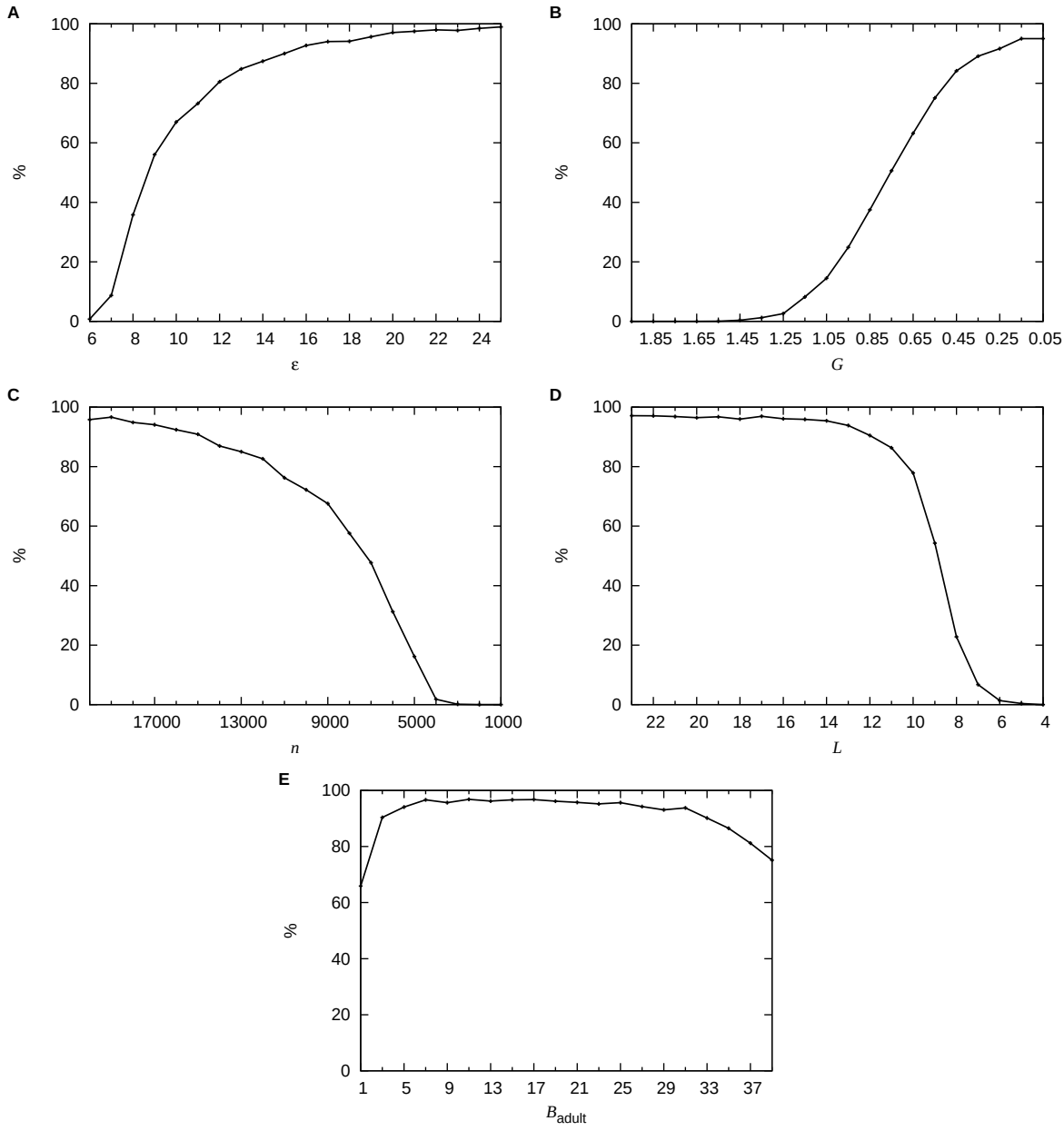



**Figure 5.1.:** Average equilibrium percentage of sexual females varying with (A) maximum consumption rate $\varepsilon$, (B) intrinsic growth rate of resources $G$, (C) population limiting factor $n$, (D) resource diversity $L$ and (E) minimum adult body mass $B_{\text{adult}}$. The parameters that are not varied are $B_{\text{adult}} = 15$, $\varepsilon = 20$, $L = 20$, $G = 0.1$ and $n = 20000$. Sexual-to-asexual mutation rate and the genetic variance of sexual offspring genotypes are kept constant at $u = 0.001$ and $V_g = 2.5^2$, respectively.

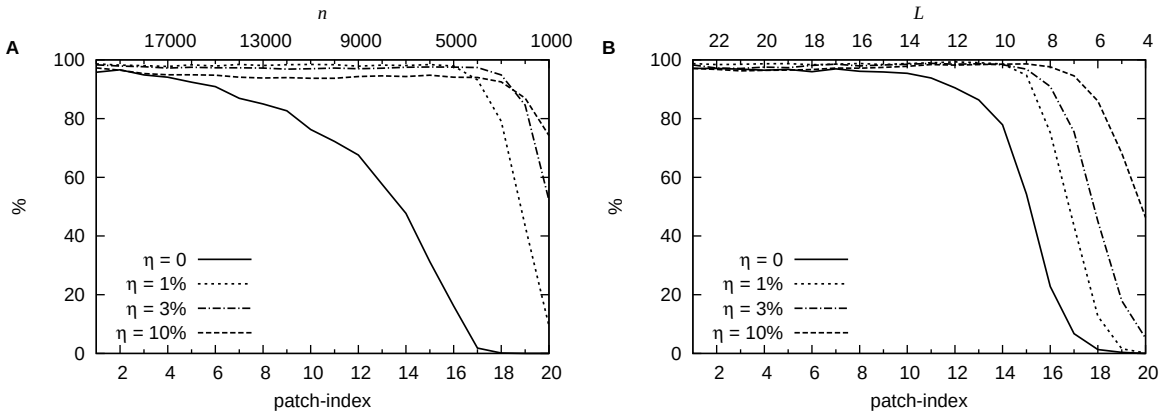



**Figure 5.2.:** Influence of the migration rate $\eta$ on the equilibrium percentage of sexual females among females in the 20 patches as varying with (A) population limiting factor $n$ and (B) resource diversity $L$. The parameters are identical to those in 5.1C and 5.1D respectively, with an added migration rate $\eta$.

individuals exploiting a broader niche spectrum and acquiring more resources, due to parents using different resources than their offspring and siblings also differing in resource exploitation from each other.

By varying the maximum consumption rate, the intrinsic growth rate of resources, and the population limiting factor (Figures 5.1A, B, C), we find that asexual reproduction wins when the level of exploitation of all resources is low. However, asexual reproduction also wins when all resources are exploited to a large extent. This happens in Figure 5.1D, where the average percentage of sexual females decreases with decreasing resource diversity, $L^2$. For instance, when $L = 8$, there are 64 niches: Since each individual feeds strongly on 9 resources, a large part of resources are covered when there are 7 genotypes in the population. Producing offspring with a different genotype is only of modest advantage, and the proportion of sexual females has sunk to 20 percent in our simulations for $L = 8$.

In Figure 5.1E we show the results of an investigation that is typical for large long-lived species with varying minimum adult body mass, $B_{\text{adult}}$. Here sexual lineages perform best for intermediate values of $B_{\text{adult}}$. If $B_{\text{adult}}$ is small, the generation time is short and the twofold cost of producing males is incurred so often that the asexual population wins more easily due to its higher production of offspring. On the contrary, if $B_{\text{adult}}$ becomes too large, the generation time is so long that also the sexual individuals suffer heavily from the exploitation of their resources. These findings confirm the hypothesis that sexual reproduction is most beneficial when it sets in at the moment when resources become scarce. When the sexual reproduction sets in earlier (i.e., when the generation time is too short), resources are not yet consumed, and there is no advantage of producing offspring that exploits different resources, but the disadvantage of producing males. When the sexual reproduction sets in later, sexual individuals suffer from resource scarceness almost as severely as asexual individuals, resulting once again in a loss of the advantage of sexual reproduction.

### 5.3.3 Geographic parthenogenesis

By arranging 20 patches along a one-dimensional chain and by assigning to them different values of the ecological parameters, we investigate the influence of a gradually changing environment in space. After birth, each individual is allowed to migrate to each neighboring patch with a migration probability $\eta$. Figure 5.2 shows the results obtained for different migration rates. When the migration rate is zero, the curves are identical to those of Figure 5.1. With increasing migration rate, the parameter range for which sexual reproduction dominates increases, because sexual migrants can counteract the local loss of genetic variance. After several generations, genotypes in a sexual population are distributed around a barycenter and together form a cloud (Fig. 5.4 of section 5.5). The cloud will move faster due to mating with migrants, improving the chance of sexual individuals to gain underutilized resources. Furthermore, by migration sexual reproduction can regain a patch from which it has become extinct.

For not too large values of the migration rate, the pattern of geographic parthenogenesis emerges: when the conditions are harsh, as manifested by high mortality or low resource diversity, asexual reproduction dominates; otherwise sexual reproduction dominates.

To ensure that our results are not due to the initial conditions chosen by us (which are to some extent arbitrary), we also run simulations where we start with 20 sexual females and 20 sexual males, with no asexual individuals. The result differs only marginally from that obtained with the initial conditions chosen before. In order to accelerate the production of asexual mutants, we set the sexual-to-asexual mutation rate $u = 0.01$, which is unrealistically high. In spite of this high value, we still find a large range of parameters where the proportion of sexual females is above 90%, demonstrating the advantage of sexual reproduction in a world of diverse resources in short supply.

## 5.4 Discussion

Based on the idea that the prevalence of sexual reproduction is due to genetically different offspring being able to consume different resources (Bell, 1982; Maynard Smith, 1971b; Williams, 1975), we developed a model for the evolution of sex in large and long-lived organisms. The model includes the two fundamental processes of virtually any living multicellular organisms, i.e., the consumption of resources for somatic growth and the investment of resources into offspring production. In unitary organisms, which grow to maturity by multiplying cells based on mitosis, resources are invested into somatic growth until reaching a certain body size, after which sexual reproduction is initiated by activation of cells in the germline (Hughes, 1989; Stearns, 1992). Remarkably, resources then are invested into the production of offspring genetically different from the parents, by the processes of meiosis and fusion with genetically different gametes (outcrossing). This change in resource investment from clonal growth during ontogenesis to offspring produced sexually after reaching maturity characterizes the life cycle of unitary organisms, i.e., most metazoan animals (Begon *et al.*, 2005; Stearns, 1992). But why this switching occurs remains unclear and presents the essence of the enigma of the maintenance of sexual reproduction. Our model for the first time includes both of these fundamental processes of virtually all living multicellular organisms. It focuses on large and long-lived meta-

zoan animals such as vertebrates that reproduce several times. The model therefore combines theories on life history evolution with theories on the maintenance of sexual reproduction. Combining these two bodies of theories and basing both of them on the consumption of resources as the main driving force are possible by building on our work presented in the previous chapter. In Chapter 2 and 3 we presented a model on the maintenance of sexual reproduction in organisms characterized by intermittent mixis, i.e., organisms that reproduce asexually except once per season when resources become limiting. This model ignored that allocating resources to somatic growth fundamentally changes life history characteristics and the fitness of organisms. Focusing on these changes, we presented a model on the evolution of life histories based on metabolic theory and explicit resource-consumer dynamics in the previous chapter. The unifying approach taken in the present model is based on the assumption that both somatic growth during ontogenesis and the production of offspring by sexual reproduction are driven by resource availability as the most important factor determining growth, survival and the mode of reproduction (Bell, 1982, 1988; Ghiselin, 1974; Williams, 1975).

Our model explicitly takes into account the dynamics of resources and the negative feedback between resource use in the current generation and the resource availability to offspring in the next generation. Similar to the model for short-lived species with intermittent mixis (Scheu and Drossel, 2007), we found that asexual reproduction predominates when mortality is high, resource diversity is low or resources regrow so fast that resource scarceness never occurs. Since in these situations there is no advantage to producing genetically different offspring, asexual reproduction performs better due to its higher productivity. By extending the model to include a spatial dimension (Ament *et al.*, 2008) and by applying a mortality gradient in space (chapter 3 and 2), we gained a distribution pattern of sexual reproduction resembling geographic parthenogenesis (Kearney, 2006; Vandel, 1928), with sexual reproduction dominating in favorable and asexual reproduction dominating in harsh environments. Together with Chapter 3 and 2 we thus have shown that the concept of a world of structured resources in short supply is recommendable. This concept results in the predominance of sexual reproduction for both modular short-lived organisms that experience sex only once per season and long-lived unitary organisms. The structured resource model thus offers a general theory for the maintenance of sexual reproduction. It combines processes and assumptions of two of the main theories on the evolution of sex, i.e., the Tangled Bank and the Red Queen, as it explicitly considers the dynamics of resource exploitation in space and feedback between resources and consumers in time.

We found that asexual individuals that mature at the same body mass as sexual individuals have a longer generation time, because they obtain less resources. This demonstrates the superiority of sexual offspring at exploiting resources. For long-lived species, the advantage of producing genetically different offspring is in fact larger than for seasonal species, because long-lived species are iteroparous and coexist with their offspring, possibly over several generations. Together, the coexisting individuals produced sexually exploit resources more efficiently than individuals produced asexually. The phenomenon that resources are exploited more efficiently in more diverse communities recently received considerable attention in experiments on functional consequences of the diversity of species (Balvanera *et al.*, 2006; Schmid *et al.*, 2009; Tilman, 2004), but also of the diversity of genetically different lineages within species (Cadotte *et al.*, 2009; Devictor *et al.*, 2010; Jousset *et al.*, 2011).

The body mass at which an individual reaches maturity is an important feature of the model. Individuals that mature at a larger body mass have the advantage that they can produce more offspring per year once they are mature, at the expense of having to wait longer before starting to produce offspring. Also, larger individuals experience lower mortality. However, all these advantages vanish when resources are depleted. Therefore, there is in fact an optimal range for the body mass in sexual populations. Somatic growth that represents asexual propagation of cell lineages should continue until resource exploitation has progressed to an extent that the advantage of producing genetically different offspring outweighs the cost of producing males. Of course, other factors not considered in this model, such as predation or the correlation between resource accessibility and consumer body mass, can favor smaller body mass in sexual organisms.

Given the fact that large long-lived organisms can adjust the relation between sexual reproduction and asexual (somatic) growth by adjusting their body mass, it might well be that in the evolutionary past of metazoan animals such as vertebrates the need to produce offspring asexually has vanished almost completely. Eventually, sexual reproduction became so hard-wired that today in mammals and birds no switching to asexual reproduction is possible any more due to genomic imprinting (Swales and Spears, 2005).

## 5.5 Appendix

This section shall help us to understand the simulation results and the advantage of sexual reproduction in greater depth. To make the dynamics of resource usage visible, snapshots are taken from animation of single simulations. Figure 5.3 and 5.4 are snapshots of a simulation with the same parameters chosen for the dotted curve in Fig. 5.2A ($\eta = 1\%$). Each figure shows four representative patches. Figure 5.3 shows the initial situation, i.e., 40 individuals in each patch of 400 unexploited niches, half sexual and half asexual with randomly chosen genotypes adapted to corresponding niches. There is no spatial structure within a patch, i.e., the coordinates of the niches in a patch have nothing to do with the spatial position. The distance between two niches measures their dissimilarity. Figure 5.4 shows the situation after 300 years in a simulation. In patch 6, 11 and 14, where sexual reproduction dominates, genotypes in the sexual populations are distributed around a barycenter and together form a cloud. The animation of computer simulation shows that the cloud moves faster with increasing patch index and decreasing population size. This is expected, since the barycenter of a smaller population is easier to drive by mating with migrants. The animation also makes the benefit of migration to sexual reproduction visible. In patch 14, for example, the local sexual population occasionally goes extinct after about two generations in case of $\eta = 0\%$, while in case of $\eta = 1\%$ the sexual population can later regain the patch via migration. Without migration the random extinctions of sexual reproduction are irretrievable, the chance is about 50% for the sexuals to win (Fig. 5.1C). With migration, however, the randomness is effectively suppressed and sexuals become dominant at equilibrium. (Fig. 5.2A). In patch 19, asexuals dominate. However, there are only four individuals (Table 5.1) and they all have the same genotype, i.e., their niches completely overlap (Fig. 5.4, the exploitation is marginal in niches that differ from the best adapted niches by more than 1 in either direction). A single niche with limited resources can only sustain a few individuals. This explains the rapid drop of population size from patch 17 to patch 18 (Table 5.1).

In patches dominated by asexual populations the genotype diversity is very low, since there is a permanent loss of genotypes via stochastic events of death. In this model, the only possibility for an asexual population to gain new niches is the sexual-to-asexual mutation. However, the mutation rate is very low.

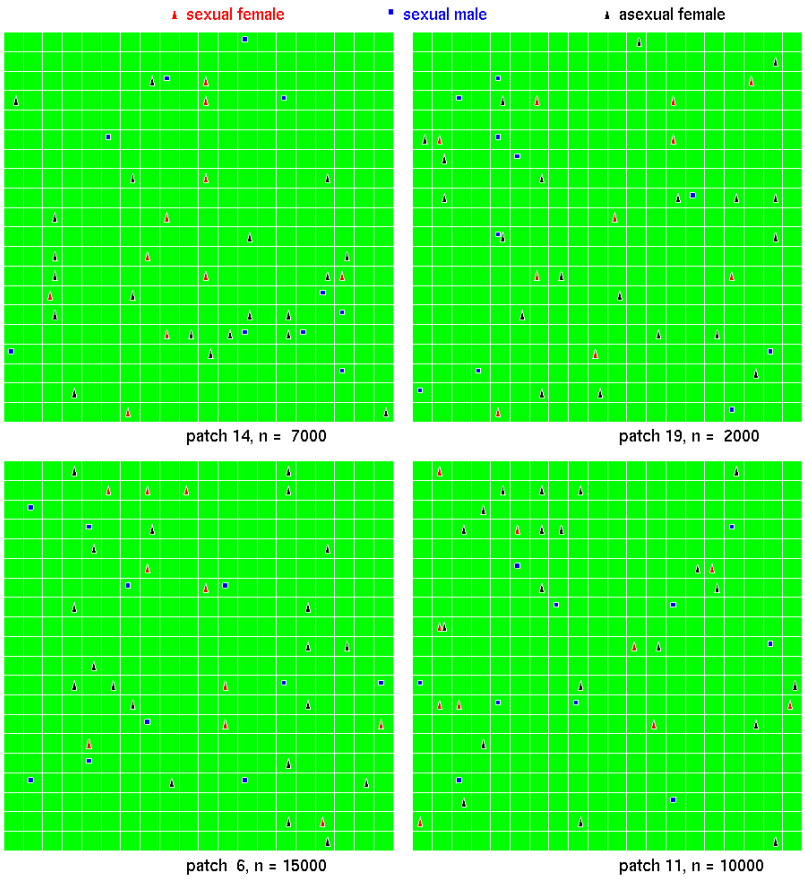



**Figure 5.3.:** Visualization of genotype and resource distribution in several patches at the beginning of a simulation with the parameters chosen for the dotted curve in Fig. 5.2A ($\eta = 1\%$). Resources are shown by green niches with the lightness representing its abundance. At the beginning of a simulation the abundance is maximum, $R_j = K_\mathrm{r}$. Sexual females are shown by red triangles that are placed in their niches according to their genotypes. Sexual males are shown by blue rectangles. Asexual females are shown by black triangles. The symbols stand for the presence of at least one individual.

To better understand the advantage of sexual or asexual reproduction, the average generation time (Fig. 5.5) and coexisting duration (Fig. 5.6) are calculated for the simulations shown in Fig. 5.1. For this purpose, simulations are terminated when either the sexual or the asexual population is driven into extinction. Figure 5.5 shows that the generation time either of the sexual or of the asexual population decreases with increasing maximum consumption rate $\varepsilon$, increasing intrinsic growth rate of resources $G$, and decreasing population limiting factor $n$. This is consistent with the result in the previous chapter (Fig. 4.3), and the reason is again that the amount of resources consumed by each individual per unit time increases with increasing $\varepsilon$, increasing $G$, and decreasing $n$. The blue curves are the average values weighted with population size, i.e., the blue curves are close to the ones of the dominant population. Figure 5.5D

**Table 5.1.:** Population size and percentage of sexuals among females after 300 years in a simulation with the parameters chosen for the dotted curve in Fig. 5.2A ($\eta = 1\%$).

| Patch | Population Size | Nr. of sexual females | Percentage of sexuals among females |
|---|---|---|---|
| 1 | 94 | 39 | 76.4706 |
| 2 | 69 | 34 | 100 |
| 3 | 76 | 38 | 97.4359 |
| 4 | 64 | 30 | 100 |
| 5 | 73 | 42 | 100 |
| 6 | 80 | 43 | 100 |
| 7 | 89 | 48 | 100 |
| 8 | 72 | 36 | 100 |
| 9 | 55 | 23 | 100 |
| 10 | 31 | 19 | 100 |
| 11 | 61 | 38 | 100 |
| 12 | 34 | 16 | 100 |
| 13 | 34 | 15 | 100 |
| 14 | 23 | 6 | 100 |
| 15 | 29 | 13 | 100 |
| 16 | 31 | 15 | 100 |
| 17 | 32 | 17 | 100 |
| 18 | 4 | 0 | 0 |
| 19 | 4 | 0 | 0 |
| 20 | 5 | 0 | 0 |

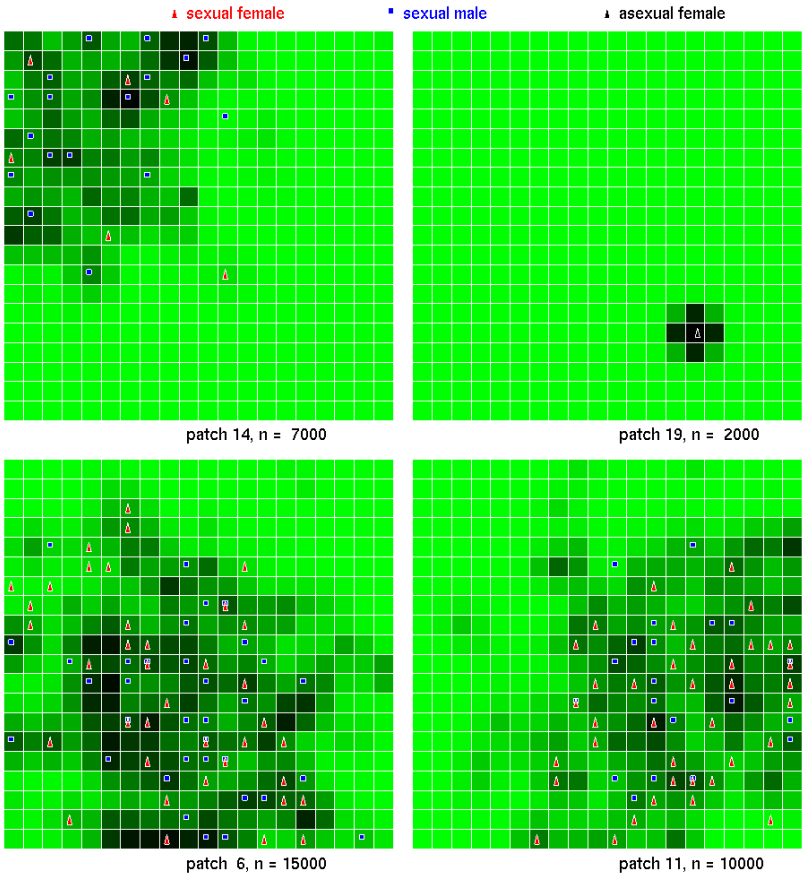



**Figure 5.4.:** Visualization of genotype and resource distribution in several patches after 300 years in a simulation with the parameters chosen for the dotted curve in Fig. 5.2A ($\eta = 1\%$). Resources are shown by green niches with the lightness representing its abundance. Sexual females are shown by red triangles that are placed in their niches according to their genotypes. Sexual males are shown by blue rectangles. Asexual females are shown by black triangles. The symbols stand for the presence of at least one individual.

shows that the generation time of sexual populations increases with decreasing resource diversity $L$. This is because of the reduction of niches resulting in more individuals coexisting in the same niche, i.e. less resources per individual. The drop from patch 19 to patch 20 is because individuals die early and do not survive for a long time after maturity. The generation time increases with increasing minimum adult body mass $B_{\text{adult}}$ (Fig. 5.5). As shown in all graphs (Fig. 5.5), the generation time of sexual populations is shorter than that of asexual populations. This confirms the advantage of sexual reproduction via producing genetically different offspring that can exploit underutilized resources. They thus gain more energy to grow faster and have a higher reproduction rate. Figure 5.6 shows the average coexisting time that is equivalent to the duration from initiation until one reproduction mode drives the other into extinction and wins the patch for itself. The coexisting time is always less than 700 years and mostly under 100 years. This fact guarantees that 1000 years are more than sufficient to obtain an equilibrium distribution of sexual reproduction. The values plotted in the area of blue grids are of acceptable statistics, i.e., the number of samples is larger than 100 (Fig. 5.7). Therefore, we only discuss the results shown in those areas. The average coexisting time is longer if the sexuals rather than the asexuals win at the end, except for the case with decreasing $L$ (Fig. 5.6D). The reason is that the asexuals, if any, have to win in the first generations where their genotype diversity is still comparable with that of the sexuals. Afterwards it is virtually impossible for the asexuals to win in a patch where high genotype diversity brings significant benefit to the sexual population. Inside the blue grid of Fig. 5.6D, the coexistence time is approximately four generations both for sexual and asexual populations. The reason here is the low resource diversity. The advantage of sexual offspring exploiting new resources is reduced, so that asexuals can also win at a later point in time. Figure 5.7 shows the number of simulations where sexual or asexual reproduction wins. When both reproduction modes are still present after 1000 years, the simulation will also be terminated. That is why, for instance, the number of victories in Fig. 5.7D summed up is less than the total number of simulations. Compared to Fig. 5.1, the sexuals performs better in Fig. 5.7. Since the simulations are terminated once sexual reproduction wins the patch, the possibility of a sexual-to-asexual mutant regaining the patch for asexual reproduction is excluded.

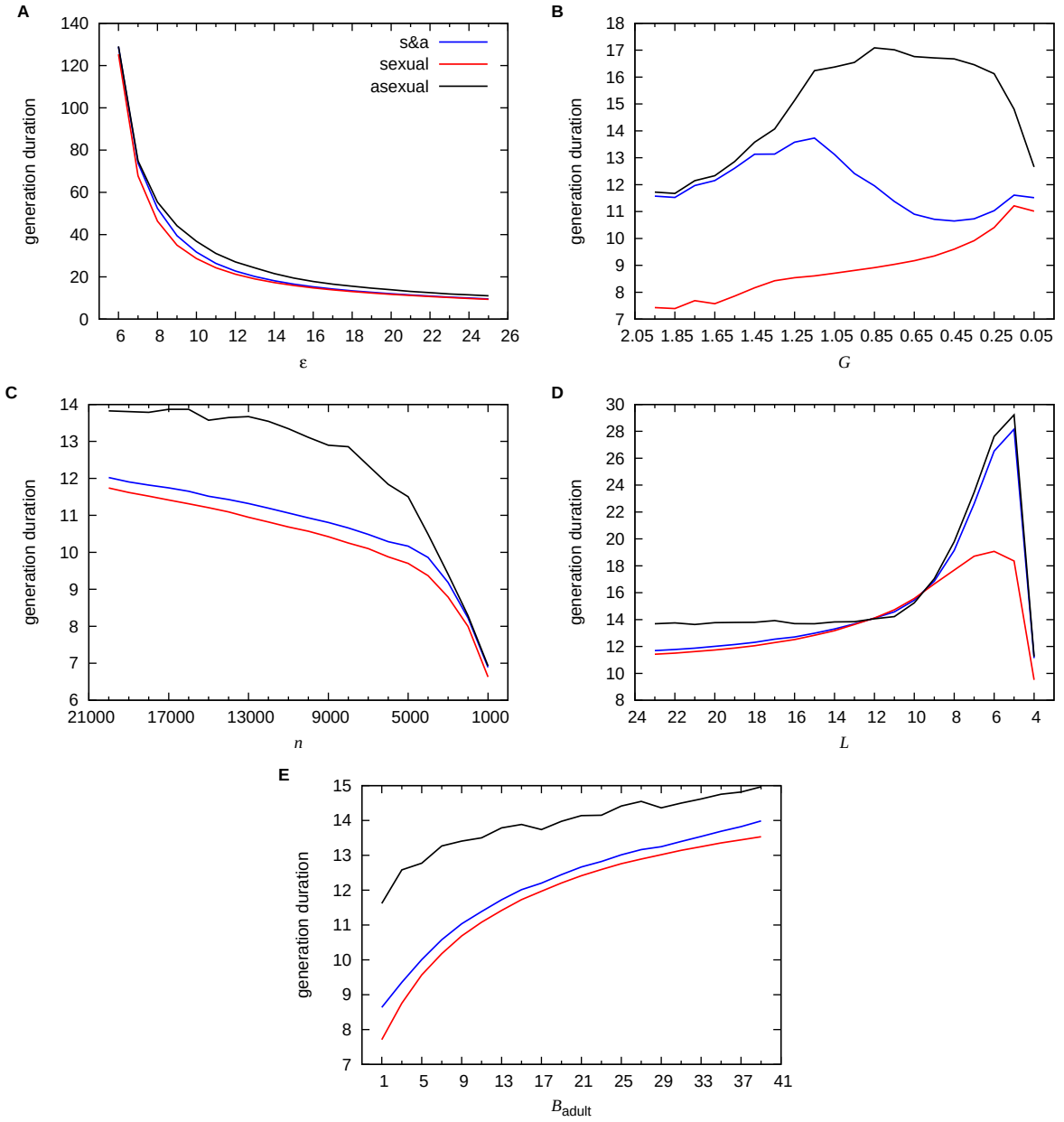



**Figure 5.5.:** Average generation duration of sexual, asexual and the mix population varying with (A) maximum consumption rate $\varepsilon$, (B) intrinsic growth rate of resources $G$, (C) population limiting factor $n$, (D) resource diversity $L$ and (E) minimum adult body mass $B_{adult}$. The curves are resulted from 500 simulations. The parameters that are not varied are $B_{adult} = 15$, $\varepsilon = 20$, $L = 20$, $G = 0.1$ and $n = 20000$. Sexual-to-asexual mutation rate and the genetic variance of sexual offspring genotypes are kept constant at $u = 0.001$ and $V_g = 2.5^2$, respectively. No migration is allowed in these simulations.

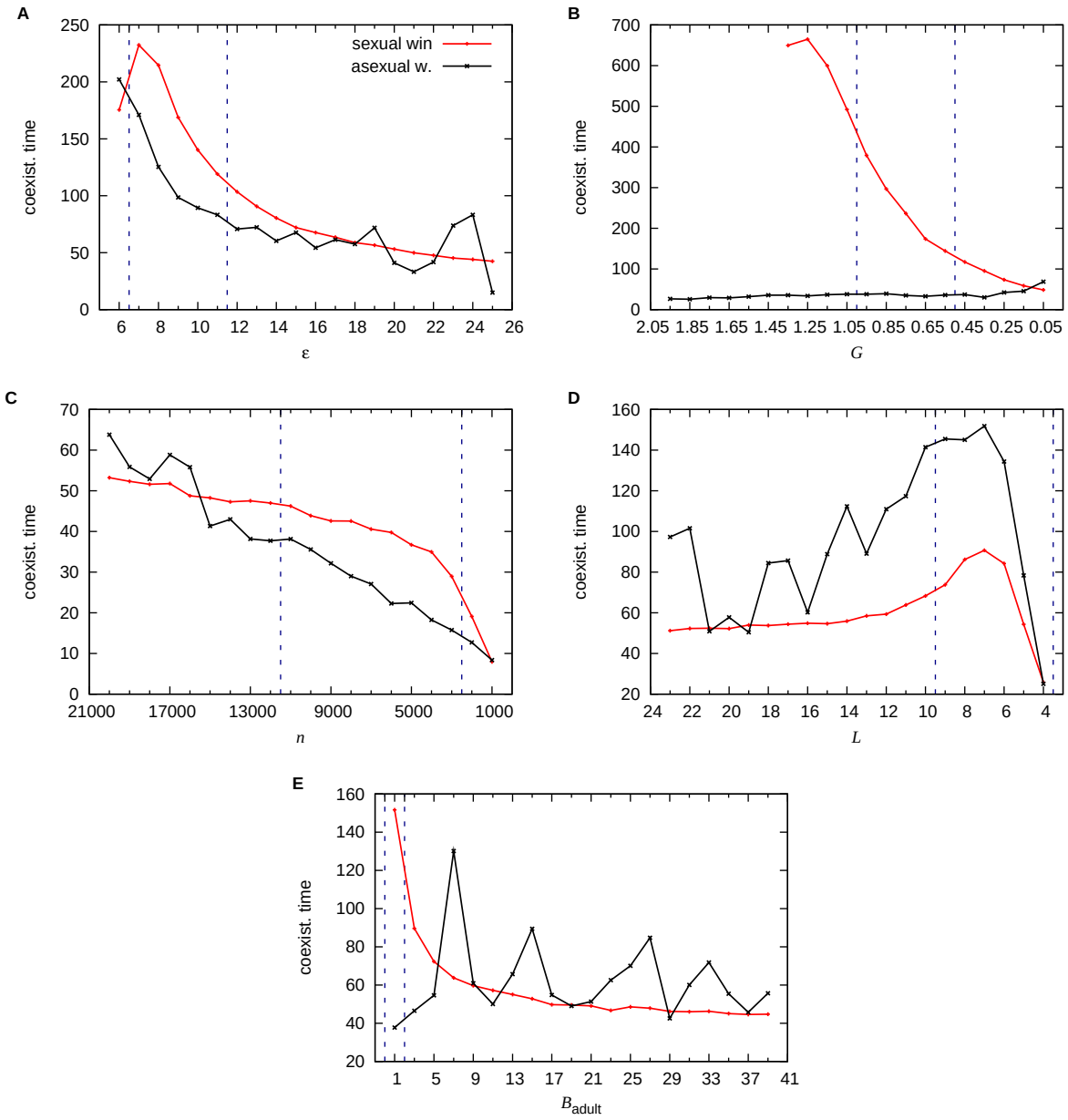



**Figure 5.6.:** The average coexisting time of sexual and asexual populations is shown separately for simulations in which sexuals or asexuals win, respectively, varying with (A) maximum consumption rate $\varepsilon$, (B) intrinsic growth rate of resources $G$, (C) population limiting factor $n$, (D) resource diversity $L$ and (E) minimum adult body mass $B_{\text{adult}}$. The curves are resulted from 500 simulations. The parameters that are not varied are $B_{\text{adult}} = 15$, $\varepsilon = 20$, $L = 20$, $G = 0.1$ and $n = 20000$. Sexual-to-asexual mutation rate and the genetic variance of sexual offspring genotypes are kept constant at $u = 0.001$ and $V_g = 2.5^2$, respectively. No migration is allowed in these simulations.

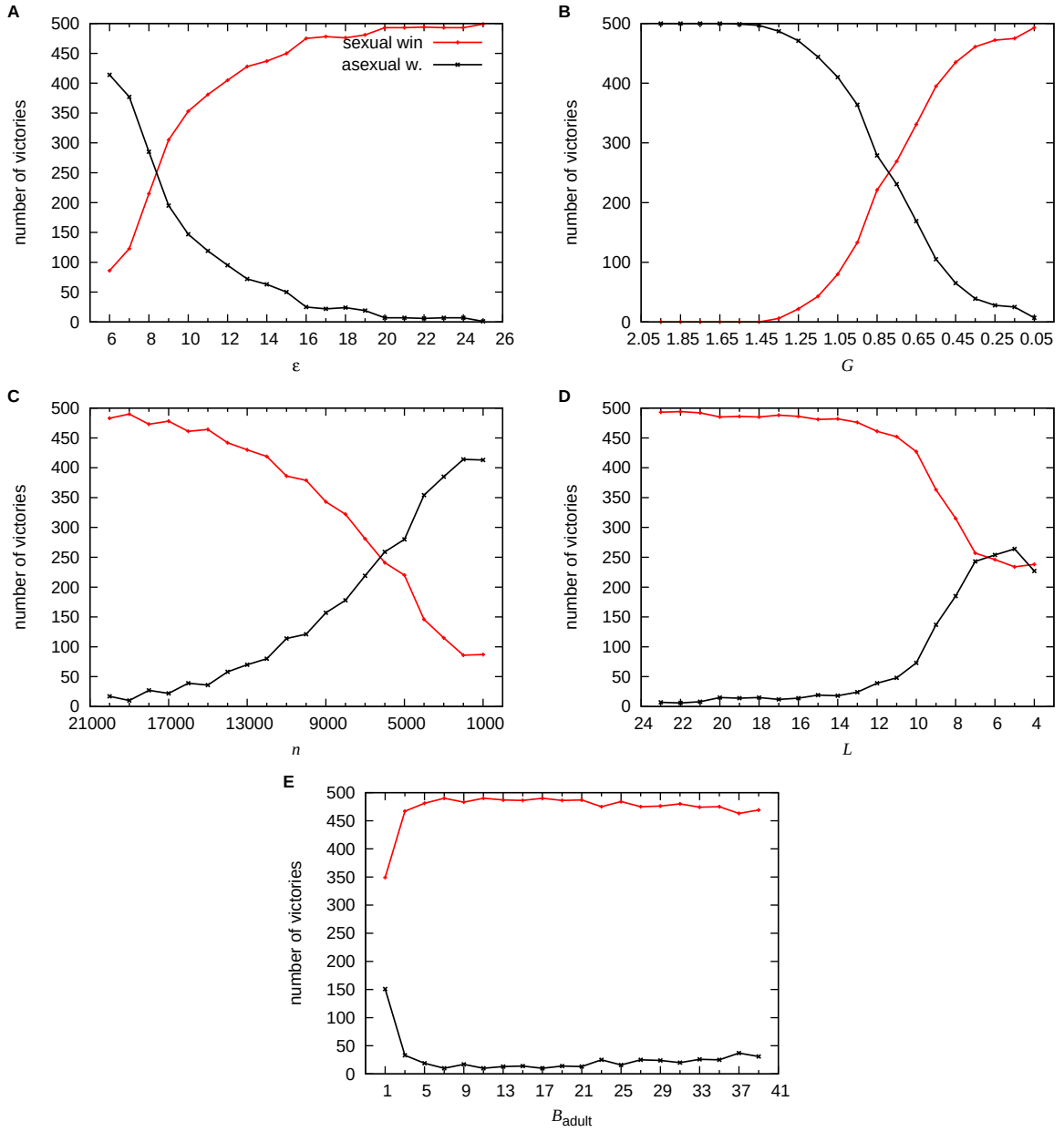



**Figure 5.7.:** Number of victories of sexual or asexual population in 500 simulations, varying with (A) maximum consumption rate $\varepsilon$, (B) intrinsic growth rate of resources $G$, (C) population limiting factor $n$, (D) resource diversity $L$ and (E) minimum adult body mass $B_{adult}$. The parameters that are not varied are $B_{adult} = 15$, $\varepsilon = 20$, $L = 20$, $G = 0.1$ and $n = 20000$. Sexual-to-asexual mutation rate and the genetic variance of sexual offspring genotypes are kept constant at $u = 0.001$ and $V_g = 2.5^2$, respectively.

# 6 Summary & Outlook

The thesis aims at explaining the maintenance of sexual reproduction by the structured resource model (Scheu and Drossel, 2007) inspired by the Tangled Bank hypothesis. The original model by Scheu and Drossel (2007) is based on a broad spectrum of limited resources that regrow slowly and a population of individuals that can consume resources covering a small fraction of the spectrum. This model is the first one explicitly taking into account the population dynamics of the resources. The model provides a large parameter range where sexual reproduction wins over parthenogenesis, even under continuously invasions of parthenogenetic clones.

My work mainly consists of two projects. In the first project, the structured resource model is spatially extended to solve the riddle of geographic parthenogenesis. Instead of a single patch, the model now includes 20 patches that are arranged in a one-dimensional chain and that are connected by migration between neighboring patches. With the spatial extension a pattern resembling geographic parthenogenesis (Vandel, 1928) is obtained at equilibrium of the geographic distribution of sexual reproduction. In patches with low mortality or high resource diversity sexual reproduction predominates, while parthenogenesis predominates in patches with high mortality or low resource diversity. The result is robust against various genetic implementations. Four different types of genetic algorithms are separately implemented in the computer simulation, and the same pattern of geographic parthenogenesis is obtained at equilibrium.

In the quantitative genetic model (Chapter 2), the dynamics of resource use in sexual populations are investigated. Due to random mating, the genotypes of the parent generation are clustered and cover only a part of the resources. From generation to generation, this cluster moves and reaches resources that have not been used in previous generations. This means that the collective niche of the daughter generation is not broader than that of the parent generation, but it has moved and includes fresh resources. The ongoing temporal change in resource use is driven by the negative feedback between resource consumption and resource availability. Furthermore, with a trait value indicating the adaptation to habitats, the model also includes the disadvantage of sex and recombination, which is to break up well-adapted genotypes. Even though, sexual reproduction is still dominant in favorable regions.

In the genetically explicit model (Chapter 3), the number of genotypes in sexual and parthenogenetic populations is investigated in order to identify the impact of limited and structured resources. The slowly regrowing resources support genotype diversity in the consumer populations. In patches representing favorable habitats, i.e., the mortality is low or the resource diversity is high, rare genotypes are promoted as they have more resources available. Sexual offspring are genetically different from their parents and siblings. Therefore, they are equally promoted by structured resources as the rare genotypes. In patches representing harsh habitats, however, rare genotypes are hardly promoted as all resources are exploited to the same extent. In case of high mortality, the resources are hardly exploited, and there is no use to produce genetically different offspring. In case of low resource diversity, there are no unutilized resources to exploit. Based on the same mechanism, sexual reproduction dominates in favorable regions

where its advantage of producing diverse genotypes overcompensates the twofold cost of sex, while it fails in harsh regions where such advantage is marginal.

The influence of migration on the distribution of sexual reproduction is investigated in both models. For the sexuals, new genetic variants are brought in from neighboring patches to the local population via migrations. These new variants can promote the movement of clusters built by local genotypes (Chapter 2), or they can prevent a decline of genetic variance of the local sexual populations (Chapter 3). For the parthenogens, migration helps asexual clones occupy niches in other patches and gain more resources. The advantage of sexual reproduction increases at first with increasing migration rate, because new genetic variants are brought in from neighboring patches. Therefore, the advantage of sexuals increases at first with increasing migration rate and then decreases as the migration rate becomes even larger.

So far, the structured resource model is tailored to short-lived species like *Daphnia* and aphids. In the second project, the structured resource model is modified and applied for long-lived organisms. This work is unique in theories of sex as it involves variation of life history traits.

As preliminary work, the consequences of metabolic theory for life histories and life history evolution are explored in a consumer-resource model. In the model with density dependent mortality the individuals have a shorter life span and a higher mortality in populations, when they use faster growing resources or have a higher consumption rate. Based on metabolic scaling individuals in populations with a larger adult body mass have a longer life span, a larger number of offspring per female, and a higher biomass density. In this consumer-resource model Cope's rule (Hone and Benton, 2005) is derived solely from the metabolic theory. As the adult body mass is allowed to evolve, it increases in time without limits. The model derives fundamental life history characteristics, such as age at maturity, number of offspring, and longevity, by combining metabolic theory with consumer resource dynamics in stationary populations. The model also has limitations due to its simplicity and abstraction of nature. We ignored the influence of age on mortality, the maximum age of reproduction, the correlation between adult and juvenile body mass, etc. Yet, it provides a null model for evaluating the role of other factors, such as predation and environmental stochasticity, and for the evolution of life history characteristics in future studies. Including environmental stochasticity, e.g., recurring catastrophic events that kill a large portion of the population, the model can explain the evolution of small adult body mass such as the phenomenon of pygmies. During the subsequent population expansion, smaller adult body masses confer an advantage due to the earlier onset of reproduction.

The role of spatial or temporal resource distribution in driving the mode of reproduction of long-lived organisms is investigated as the last project in this work. In Chapter 5, the advantage of sexual reproduction in long-lived organisms is evaluated in localities with different ecological properties. Sexual reproduction again wins in patches with low mortality and high resource diversity. The advantage of producing genetically different offspring is more significant in long-lived organisms. Here, individuals produce more than once per life time, and they often live with their offspring at the same time. Sexually produced offspring can use different resources from those of their parents and thereby avoid direct competition for resources with their parents. Parthenogenetically produced offspring, however, suffer from intense competition with their parents in addition to competition between siblings.

The body mass at which an individual reaches maturity is an important feature of the model. An optimal range is observed for the body mass of sexual populations. From the view of metabolic theory, somatic growth, which represents asexual propagation of cell lineages, should continue until resource exploitation has progressed to an extent that the advantage of offspring exploiting different resources outweighs the cost of producing males. Here sexual lineages performed best for intermediate values of the body mass at maturity. If the body mass at maturity is small, the generation time is short and the twofold cost of producing males is exerted too often for the sexual reproduction to win. On the contrary, if the body mass at maturity becomes too large, the generation time is so long that also the sexual individuals suffer heavily from the exploitation of their resources. This demonstrates the fact that large long-lived organisms can adjust the relation between sexual reproduction and asexual (somatic) growth by adjusting their body mass. It might well be that in the evolutionary past of animals, such as vertebrates, the need to produce offspring parthenogenetically has vanished almost completely. This model thus provides an explanation for the absence of parthenogenesis in mammals and birds based on evolutionary and ecological aspects.

In summary, the structured resource model connecting the Tangled Bank and Red Queen hypotheses explains the maintenance of sex and geographic parthenogenesis in short- and long-lived organisms. The work reproduces, for the first time, the distribution pattern resembling geographic parthenogenesis. Furthermore, the model for long-lived organisms sheds light on understanding the absence of parthenogenesis in mammals and birds from an ecological perspective. The Tangled Bank hypothesis that inspired this work evidently has a promosing potential in generally explaining the enigma of sexual reproduction. As sexual reproduction is induced by resource scarceness the structured resource model, in addition to explaining the maintenance and dominance of sexual reproduction, has the potential to explain the origin of sex.

## Glossary

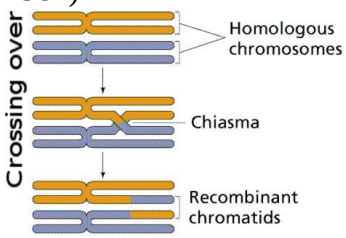
**Adaptive radiation.** Evolution of an animal or plant group into a wide variety of types adapted to specialized modes of life. - http://www.britannica.com, page 10

**Allele.** One of the two or more **genes** which may occupy the same site (**locus**) on a chromosome. (Bell, 1982)

**Chiasma.** A region of contact between **homologous chromosomes** during **meiosis** in which there is an exchange of homologous parts between non-sister **chromatids**. Cf. **crossing-over**. (Bell, 1982), page 6

**Chromatid.** One of the two identical replicates of a chromosome formed during nuclear division. (Bell, 1982)

**Crossing over.** Usually, the exchange of genetic material between non-sister **chromatids** of **homologous chromosomes** by symmetrical breakage and reunion during **meiosis**. (Bell, 1982)




- http://www2.estrellamountain.edu

**Diallelic.** Having two possible **allelic** states. (Bell, 1982), page 42

**Epistasis.** The interaction between the **genes** at two or more **loci**, so that the **phenotype** differs from what would be expected if the loci were expressed independently. - http://www.blackwellpublishing.com, page 3

**Gene.** The unit of inheritance; a small part of a chromosome producing a certain protein and separated from adjacent parts producing different proteins. (Bell, 1982)

**Genetic drift.** Random changes in gene frequencies in a population. (Ridley, 2004, p.684), page 14

**Genetic recombination.** The change in the relationship between **loci** on the same chromosome caused by **crossing-over**. (Bell, 1982), page 2

**Genomic imprinting.** The **parent-of-origin** specific gene expression. Genomic imprinting results in only one inherited copy of the relevant imprinted gene being expressed in an embryo. (Swales and Spears, 2005), page 17

**Genotype.** (1) The **allelic** state of any specified number of **loci** in a given individual. (2) The genetic potential realized in the **phenotype**. (Bell, 1982)

**Haploid.** Possessing a single set of chromosome. (Bell, 1982), page 3

**Homologous chromosomes.** A pair of chromosomes in which one member of the pair is obtained from the organism's maternal parent and the other from the paternal parent; found in diploid cells. - http://www2.estrellamountain.edu

**Hybrid.** An offspring resulting from the cross between parents of different species or subspecies. - http://www.biology-online.org

**Hybridization.** The act or process of mating organisms of different varieties or species to create a **hybrid**. - http://www.biology-online.org, page 23

**Intermittent mixis.** A more precise term of cyclical parthenogenesis suggested by Bell (1982)., page 7

**Iteroparous.** A species is considered iteroparous if it has many reproductive cycles over the course of its lifetime, and semelparous if it reproduces a single time before it dies. In plants, the term polycarpy is equivalent to iteroparity, and monocarpy is equivalent to semelparity. - http://semelparity-and-iteroparity.co.tv, page 61

**Locus.** A site on a chromosome at which different **genes** are **allelic** to one another. (Bell, 1982)

**Meiosis.** A single or (much more often) a sequence of two nuclear divisions during which **ploidy** is halved, typically involving **genetic recombination** through **crossing-over** between **homologous chromosome**. (Bell, 1982), page 2

**Metabolic rate.** The rate of **metabolism**. (Brown *et al.*, 2004), page 16

**Metabolism.** The biological processing of energy and materials. Organisms convert energies that are taken from the environment to other forms within the body and allocate energies to survival, growth, and reproduction. (Brown *et al.*, 2004), page 16

**Metazoan animals.** (1) Multicellular, mitochondrial eukaryotes. Today Metazoa encompasses all animals with differentiated tissues, including nerves and muscles. - http://microbewiki.kenyon.edu

(2) Any member of the kingdom Animalia, a group of many-celled organisms that differ from members of the two other many-celled kingdoms, the plants and the fungi, in several ways. - http://www.britannica.com

**Mitosis.** A single nuclear division typically resulting in the exact replication of the genome. (Bell, 1982)

**Mixis.** The rearrangement of genetic material through **meiosis** or syngamy or (usually) both, almost always resulting in the production of one or more new organisms differing genetically from one another and from their parents. (Bell, 1982), page 1

**Parent-of-origin studies.** An analysis used to determine whether a particular chromosome or segment of DNA was inherited from an individual's mother or father. - http://ghr.nlm.nih.gov

**Parthenogenesis.** Asexual reproduction that involves development of a female (rarely a male) gamete (sex cell) without fertilization. It occurs commonly among lower plants and invertebrate animals, particularly rotifers, aphids, ants, wasps, and bees. An egg produced parthenogenetically may be either haploid (i.e., with one set of dissimilar chromosomes) or diploid (i.e., with a paired set of chromosomes). - http://www.britannica.com/EBchecked/topic/444810/parthenogenesis, page 1

**Phenotype.** Any measurable characteristic of an organism. (Bell, 1982)

**Ploidy.** A term referring to the number of sets of chromosomes. Haploid organisms/cells have only one set of chromosomes. - http://www2.estrellamountain.edu, page 3

**Polymorphic.** Diverse: the occurrence of different **phenotypes** among members of the same population. (Bell, 1982), page 5

**Polyploidy.** The condition in which a normally diploid cell or organism acquires one or more additional sets of chromosomes. In other words, the polyploid cell or organism has three or more times the haploid chromosome number. Polyploidy arises as the result of total nondisjunction of chromosomes during **mitosis** or **meiosis**. - http://www.britannica.com, page 23

*K*-**strategy.** Energies are mainly allocated in survival, e.g. large adult body size and delayed maturity, or large newborn offspring size and reduced number of offspring.
*r*-**strategy.** Energies are mainly allocated in reproduction, e.g. small adult body size and early maturity, or small newborn offspring size and large number of offspring., page 16

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### Conference Contributions

- Song, Y., Ament, I., Scheu, S., and Drossel, B. 2009. Competition between sexual and asexual reproduction: geographic parthenogenesis in structured resource space. In *Proceedings of DPG Spring Meeting of the Condensed Matter Section*, BP 17.38, Mar. 22-27, 2009, Dresden. German Physical Society. (Poster)
- Song, Y., Ament, I., Scheu, S., and Drossel, B. 2009. A model for geographic parthenogenesis, in *Proceedings of the Congress of the European Society for Evolutionary Biology*, Symposium 14.5, Aug. 24-29, 2009, Torino. European Society for Evolutionary Biology. (Poster)
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Hiermit versichere ich, die vorliegende Dissertation ohne Hilfe Dritter nur mit den angegebenen Quellen und Hilfsmitteln angefertigt zu haben. Alle Stellen, die aus Quellen entnommen wurden, sind als solche kenntlich gemacht. Diese Arbeit hat in gleicher oder ähnlicher Form noch keiner Prüfungsbehörde vorgelegen.

Darmstadt, den August 10, 2011

(Y. Song)